VOL. XV, PARTS III & IV *Published* 21 *March* 1931

The British Mycological Society

(*Recognosce notum, ignotum inspice*)

TRANSACTIONS

Edited by

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Price to non-members, Fifteen Shillings

CAMBRIDGE UNIVERSITY PRESS
LONDON: FETTER LANE, E.C. 4
ALSO
H. K. LEWIS AND CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(AGENT FOR THE UNITED STATES)
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TOKYO: THE MARUZEN COMPANY LTD.

PRINTED IN GREAT BRITAIN

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RECENT LICHEN LITERATURE.

By A. Lorrain Smith, F.L.S.

Introduction.

We cannot begin our review of recent literature without paying homage to the distinguished lichenologists who have recently passed away. Edvard Wainio of Finland has had a long and remarkable career in Lichenology, having made that subject his main study from his student days. He was not only in the forefront as a systematist, he was also a brilliant exponent of the problems and of the reasoned arrangement of these symbiotic plants. Through his many standard works on lichens from all quarters of the globe he had reached a commanding and trusted position. His first paper—on Finnish lichens—was issued in 1878. In 1901 was published his account of the lichens collected by Welwitsch in W. Africa, and entrusted to him by the Trustees of the British Museum. His most recent publications are recorded in the following pages.

American lichenology has also suffered heavily by the loss of Professor Bruce Fink and of G. K. Merrill. Both confined their studies chiefly to the Western Continent—a field wide enough indeed. Merrill had achieved a great reputation though he has left no outstanding work. Bruce Fink published many years ago his *Lichens of Minnesota* (1910), a most careful and valuable text-book. We regret his loss the more, as he was compiling material for a Lichen Flora of America.

Several important works have appeared during the last few years. Wainio—who had recently changed his name to Vainio—had issued in 1927 the third volume of *Lichen Flora of Finnland* on the Coniocarpeae. They are a difficult order, and Vainio has made a number of changes in genera and species—not a few being relegated to Fungi. We are told that he chose to begin his *Flora* with the least known groups, in the fear that he might not live to finish his task.

Migula's *German Flora* is advancing; it will be a large and imposing work when finished, with an abundance of coloured illustrations. A. Zahlbruckner has reached volume VI of his *Universal Catalogue*, a work indispensable to all serious students of lichens. His last issued parts have dealt with Parmeliaceae and the numbers listed reach 11,800 and more.

Two text-books have been prepared for the use of students, both unfortunately somewhat incomplete. The first—by Anders (1928)—is restricted to the larger foliose and fruticose lichens of Central Europe. Some three hundred species have been repre-

sented by photographs. The second—by A. H. Magnusson (1929)—has followed the same lines for Scandinavia, dealing as it does with the larger lichens only, though, in a genus like *Dermatocarpon*, it involves the selection of the more evident forms only. Both books give an account of the nature and structure of the lichen plant and both are amply provided with keys to genera and species. There should also be noted a proposed work by Choisy, of which the first contributions have appeared. There are many illustrations of lichens and their structure, some coloured. He has given his views on classification, dividing the whole class into groups according to the type of spermogonia. There has been recently announced the publication of Keissler's contribution to Rabenhorst's *Kryptogamen Flora* (1930) on lichen fungal parasites. He has been the chief authority for these since the lamented death of L'Abbé Vouaux in the war. Students will anticipate with confidence the opportunity of consulting the work.

I have also to place on record the article "Lichens" contributed by me to the recent edition of the *Encyclopædia Britannica* (1929).

The Lichen Thallus.

Gonidia. A paper was published in 1925 by Uphoff stating that the purple colour of *Chiodecton sanguineum* was due to colour-bacteria which functioned as symbionts. Suessenguth (1926) finds that the colouring matter is provided by the lichen-acid, chiodektin, which he obtained in crystalline form. *Chiodecton* possesses normal gonidia.

The question as to the true conception of the common green gonidium is still debated. Werner (1927) rejected the name *Trebouxia* Puy. as redundant and he retains *Cystococcus*, described by Chodat as having a stellate chromatophore. Paulson (1929) has made a further elaborate and exact microscopic study of the chromatophore; he proves by skilful photomicrography—thus securing the exact centre and focus of the image—that the chromatophore in normal healthy conditions is of regular outline resembling more nearly *Chlorella* than *Trebouxia* or *Cystococcus*. In recent culture work by Jaag the matter is again threshed out: in his preliminary papers (1928, 1, 2) he gives a general account of the gonidium in culture conditions, with stellate chromatophores and with formation of autospores and zoospores. As zoospores have never been observed within the lichen, one can only conjecture what influence has inhibited the production of these bodies within the thallus, and that the gonidium has reverted to ancestral characters in the freer surroundings and perhaps richer nutrition on the culture plate.

Jaag has also demonstrated an astonishing diversity of species

or strains as shown in cultures. He experimented with the gonidia of *Parmelia perlata* collected from four different trees at four different—though not greatly distant—localities: there were developed in the cultures certain superficial characters different in each case. We are forced to the conclusion that some repression within the *Parmelia* due to locality or exposure, etc., had influenced the gonidium, or we must assume that the gonidium, met with by each thallus at the beginning of its growth—though the same species, was in each case a different strain or form. *Parmelia perlata* is mainly propagated by soredia which assures the gonidial inheritance, but fortuitous association from the open must be reckoned with; it has been again confirmed by Goebel (1926, 3) in *Peltigera aphthosa*, by Bachmann in several of his papers (on Cladoniae) and by Tobler (1927) in *Baeomyces*. In a later paper (1929) Jaag contrasts the gonidia of *Parmelia* with those of *Cladonia*, the latter were somewhat elongate, while those of *Parmelia* were of a rounder form, though the distinction was not constant. He also found that the gonidia of *Cladonia* squamules were smaller than those towards the tip of the podetium: one is, therefore, inclined to treat as of minor specific importance the variations recorded between one culture strain and another. It would be of great interest to ascertain if any variation would occur in cultures of *Cystococcus* from free algae taken from different trees in four different localities. We might thus get a clue to the significance of the "strains." In Jaag's cultures autospores and zoospores developed freely, with fusion of the latter and with fusion of gametes.

Werner had described a number of new *Cystococcus* species among the gonidia of Cladoniae. Jaag (1929) has added others both in *Cladonia* and *Parmelia*, but differences were only discernible in cultures. It might be inferred from these results that each lichen species or even specimen included a different algal species, so that, as Jaag remarks, a lichen is distinguished not only by morphological characters but by specific gonidial characters. Jaag's notes on temperature, water supply and illumination are important: the gonidia could more easily endure cold than heat, and grew well at o° C., which explains the luxuriant growth of lichens in regions of extreme cold. Intense illumination retarded gonidial development and induced decoloration, with a tendency to yellow. This seems to be reflected in desert lichens where the gonidia are often distinctly yellow. Lucy Howland, in experimenting with the alga *Trentepohlia aurea* (also a lichen gonidium), found that it resisted drought for long periods and thereafter absorbed water rapidly.

Lichen Hyphae. Werner (1927, 3) has extended his culture studies to a consideration of the equilibrium between the two

symbionts, and he has given the results following the use of varying salts, organic and inorganic, in his media. He notes the power of the hyphae to liquefy gelatine which, he considers, proves their saprophytic character. Danilov (1927 and 1929) noted the abundant gelatinous formation in *Nostoc* gonidia serving for the nourishment of the hyphae. Hollerbach (1928) also remarks on this character in his account of *Collema Ramenskii*. There has been no suggestion of parasitism in blue-green forms.

Symbiosis. The symbiotic theory concerning the lichen thallus, though constantly disputed, still holds the field. Frey (1929) has observed that the more close the relationship between the two symbionts, the more definitely does the plant become a distinct and stable organism; all special thalline structures, he claims, justify this view of lichens. Bachmann (1927) also gives the support of constant careful observation: in *Cladonia* and in *Diploschistes*, with the arrival of fortuitous algae from the open, there was renewed activity of the hyphae, and excrescences due to healthy active growth were formed on the lichens and acted as isidia in increasing the area of assimilation. Tobler (1928), in his study of *Baeomyces*, noted the ready acceptance of alighting algae with healthy stimulus to both constituents. Darbishire also (1927), in his study of Cephalodia, confirms the theory of symbiosis: he could find no trace of parasitism.

E. J. Fry (1928) has, however, challenged the symbiotic condition in her examination of *Lecania candicans*, a crustaceous rock species. She has found that the hypha, in close contact with a gonidium, sends out a slender haustorium which, by mechanical action, pierces the cell and uses up the contents; autospores, even within the outer gonidium wall, are pierced. The emptied cells lie mainly in the upper cortical region and are gradually discarded by exfoliation. She claims to have established a true case of parasitism of hypha on alga, although she allows that the condition may not be universal. Werner (1927) had noted in his combined artificial cultures that the gonidia were occasionally pierced though not injured, but he remarks that, after a time, the hyphae seemed to lose the habit of symbiosis and parasitised the algae when these were in abundance.

In his discussion of symbiosis, Tobler (1928) has stated that the presence of acids is an expression of complete symbiotic life: *Xanthoria* spp. for instance have reached stable conditions, though liable to be affected by changes of light and shade. With regard to acids and chemical reactions he deprecates too great dependence on them as determining characters, as a comprehensive knowledge of growth conditions, ecology, etc., is also necessary.

Danilov (1929) also touches on the question of symbiosis. He made an artificial laboratory culture of *Leptogium Issatschenkii* Elenk. during a period of four years on an agar nutritive solution. A humid atmosphere was unfavourable in its influence on the form of the thallus changing it from a flat to a more upright form. In the ordinary atmosphere of the laboratory the combined plant grew with the same rapidity as *Nostoc* alone, and new plants grew from mere shreds of fungus and alga combined. A constant humidity induced a wart formation. Danilov found that the hyphae were nourished by the mucilage of the alga, and that at the first stages of growth the alga was dominant, equilibrium followed and finally the fungus, becoming the more important, formed not only the cortex and the fructification but took the lead in new thalline outgrowths. If the symbiotic union was enfeebled the gonidia developed purely algal colonies but only as long as the algae were young and vigorous; with age the power of growth declined. Danilov recognises symbiosis as a "condition of mobile equilibrium."

Parasymbiosis and Parasitism. The relation to the lichen host of presumed fungal parasites is again receiving attention. In not a few cases it has been proved that hyphae of the alien plant form a normal symbiotic union or parasymbiosis with the gonidia of the host—as has been demonstrated in *Buellia* (*Abrothallus*) *Parmeliarum*—no injury being done to the host plant. Werner (1928) contributes a study of *Celidium stictarum*, generally regarded as a fungus parasitic on *Sticta*, *Lobaria*, etc. He found that it was a case of true parasymbiosis and that the gonidia, instead of suffering, were excited to increased growth; the hyphae even united with the *Nostoc* cells of the internal cephalodia, a condition he terms "pseudoparasymbiosis." No piercing of the gonidia was seen. In another paper Schaechtelin and Werner (1928) describe what they call an astounding case (*un cas foudroyant*) of parasymbiosis. A fungus, *Homostegia Piggotii*, not only invades the host, *Parmelia omphalodes*, but the dark-coloured hyphae take possession of the gonidia, replacing the normal lichen hyphae. The soredia of the lichen are also invaded and so disseminate both organisms.

Morphology.

Structure. Bachmann has given a series of studies on crustaceous lichens. As regards the *Sarcogyne* section of *Biatorella* (1927) he has placed it in the lecanorine genus *Acarospora*, though the apothecia are lecideine. There are two distinct groups in the section—endolithic on limestone and immersed in the rock; and exolithic, superficial, on a siliceous substratum, the latter with a large gonidial zone and large-sized gonidia, thus

confirming views already put forth that the hyphae demand more sustenance on acid rocks, hence the need for more assimilation. He has also described the structure of three closely allied Porinae (1929), in all the thallus is only a thin layer—with *Trentepohlia* gonidia—on the rock substratum. The differences consist in the depth of the gonidial layer—in one with an epinecral layer of dead cells, in the others with a hyponecral layer. In yet another study (1929) he describes with equal minuteness the epilithic thalli of two Verrucariae—*V. acrotella* with a scanty thallus and abundant perithecia and *V. aethiobola*, more exclusively calcicolous, with rhizinae that entered the substratum, but developed neither oil hyphae nor sphaeroid cells. From Edouard Frey (1929) we have an elaborate account of Umbilicariaceae. He justifies the use of that name as having precedence of Gyrophoraceae. Incidentally he discusses the terms in use as regards hyphal structure—plectenchyma, proso- and paraplectenchyma; he also adds "Schwamm" or hyphal plectenchyma to designate loose medullary structures. The tissues of the plants dealt with are very dense right through the thallus—the density enabling them to brave the intense cold of their natural habitats. Notes on structure also accompany Frey's description of his new genera (1929) *Lecanorella* and *Tominiopsis*: in both there is an all-pervading tissue of minute cells, not only in the thallus but also in the hypothecium and thalline margin. *Lecanephebe*, also new, is distinguished by a central strand of hyphae in the narrow thalline lobes.

Deformations. In lichens as in the higher plants deformations or galls may be caused by fungi or by animals attacking the plant. Bachmann (1926) has described as "witch-brooms" a condition induced in *Cetraria aculeata* by a Hyphomycete, *Sporotrichum Lettanianum*. The fungal hyphae caused abnormal growth and they also destroyed the medullary hyphae and the gonidia. In *Cladonia amaurocrea* (1928), a minute Pyrenomycete, *Didymella Sanstedii* had invaded the tissue but with less harmful effect. There was a shortening and widening of the podetia with a multiplication of the lateral branches, but in this case there was even an increase in the gonidial layer. In other papers (1928, 1, 2) Bachmann describes the settling of fungus spores on the podetia of *Cladonia amaurocrea*, *C. gracilis* and others, with the germination of the spores and the formation of horse-shoe galls by the mycelial hyphae which travel over the surface or pierce the podetia, finally the formation of Ascomycetous fructifications. In a further communication (1928, 2) he describes gall formation on the squamules—usually the under surface—the wart-like galls inducing increased algal formation; the fungal fructification was not determined. Isolated nests of

algae on these galls produced squamules differing in no way from normal squamules. Other instances of galls due to recognised fungi are given in a later publication (1929, 3)—*Sirococcus lichenicola* parasitic on *Cladonia amaurocrea* and *Metaspheria superveniens* on *Parmelia conspersa* and *Xanthoria parietina*.

Instances of galls due to the attacks by animals are described by Bachmann (1929, 3) in *Cladonia ochrochlora* and in *Ramalina fraxinea*. There was no destruction of either symbiont, but some exciting influence on the tissues resulted in the formation of distorted and unnatural growth. Remains of insects were found in the interior of the galls, but it was impossible to recognise the invader. Fruit formation is hindered by the presence of fungi in *Cladonia amaurocrea* (Bachmann, 1929, 2) and by mites in some Pertusariae. A different type of false galls "Scheingallen" arises in the lichen itself, as in *Cetraria glauca*, where pycnidial growths resemble isidia, and in *Parmelia conspersa* cause an unusual thalline development.

Cyphellae. Goebel (1926), in a paper on Java lichens, remarks on the large number in tropical lands that are supplied with definite breathing pores, as cyphellae, pseudocyphellae or as openings of various kinds. The consideration of these bodies is closely bound up with aeration. In order that they may function properly, they must be in a dry condition and this, as Goebel has pointed out, is secured by the presence of lichen acids: if these are dissolved out the opening becomes blocked with moisture. Oxner (1929) has found that *Cetraria cucullata* and *C. nivalis* possess pseudocyphellae: the lichens were collected on the tundra in extreme north-east Asia. They had been described as lacking these aeration organs.

Cephalodia. Darbishire (1927) has traced the development of cephalodia on *Peltigera aphthosa* from the first entanglement of *Nostoc* colonies in the cortical hairs of the lichen, with the subsequent pushing up of the hyphae immediately below. A secondary cortex of the cephalodium is formed by hyphae also from the parent thallus. As the new structure spreads the underlying tissues gradually decay, but at a later stage hyphae grow out and cling round the cephalodium almost like a prothallus, thus securing a closer connection between thallus and cephalodium. Goebel (1926) has re-examined *Peltigera lepidophora* and upholds Linkola's view that the outgrowths from the thallus are of isidial nature.

Soredia and Isidia. Gyelnik (1927) in his studies of *Peltigera* makes special reference to sorediate or isidiose varieties. He has delimited several new species and forms distinguished by the presence or absence of these bodies. The Moreaus (1926) describe the granules so frequent in Collemaceae as "Collemae papillae,"

and distinguish these from true isidia of other lichens. They also give special attention to the isidia of *Parmelia scortea*: these, they find, originate by a rising of the upper cortex as a minute pustule; the cortex breaks and a small column of tissue emerges, the upper cells of which become dark in the sunlight. This "scorteal" structure may be simple or branched. A similar type of development occurs in the isidia of *Parmelia saxatilis*. The authors find this growth process repeated in the formation of the *Cladonia* podetium*.

A peculiar type of isidium—internal and corticated—has been discovered by Garside (1929) in *Siphula tabularis* from Table Mountain, Cape Town. The stalks—podetia—become flattened and verrucose at the tips owing to isidial outgrowths which start development in the gonidial zone, and acquire a surrounding cortex before they emerge and scatter to form new plants—the only form of propagation in this lichen. Garside terms these structures "endoisidia."

Reproduction.

Fructification. Apothecial development in *Collema* has been re-examined by M. and Mme Moreau (1928) with all the appliances of modern technique. They found that the young coiled ascogonium was composed of uninucleate cells which, later, are in communication by perforation of the dividing walls. As development proceeds the cells thus become multinucleate up to six nuclei in a cell: these cells produce ascogonial hyphae finally with binucleate cells and bearing the asci. They found no evidence of Stahl's theory of fertilisation by spermatia and trichogynes: many ascogonia have no trichogyne, and, if present, it rarely reaches the surface of the thallus. Spermatia take no part in fertilisation. In *Peltigera* and *Solorina* spp. they demonstrated the early arrival of the multinucleate stage of the ascogonial cells; the ascogonial hyphae, at first multinucleate, by cell septation became binucleate. These conclusions agree with the views held by most modern lichenologists, but it is well to have the question again examined by such expert workers. We note, however, that Kniep (1928) has reverted to the Sachs's view of fertilisation by trichogyne and spermatia.

In a study of *Lecidea turgidula* and *L. lithophila*, Choisy (1927) observed that the young asci were the terminal cells of ascogenous hyphae. He saw no clamp connections nor any bending back of the tip cell, as described by the Moreaus (1925), in a previous paper.

In a very different lichen, *Umbilicaria pustulata*, Werner (1928) has demonstrated that the ascogonia begin in small

* See under Phylogeny, p. 205.

cushions of densely packed cells and that from each cushion arises what he terms a "true" trichogyne—presumably, as he considers, an agent in fertilisation. These ascogonia become transformed to ascogonial hyphae, and finally asci are formed. In *Gyrophora cylindrica* and *G. crosa* there were several trichogynes for each ascogonium. He has also noted the occurrence of spermogonia with sterigmata and spermatia of the *Sticta* type. Werner failed in all attempts to germinate the spores. Frey also contributes a study of *Gyrophora* apothecia—of the gyrose lines of the disc. He compares these formations of sterile tissue with the development in *Lecidea umbonata*, the umbo of the apothecia being also a protrusion of vegetative tissue.

Spores. Abbayes followed the spore division in a species of *Bilimbia*, comparing the stages of septation with those in *Graphis* spores. In *Bilimbia* it began at an early stage with a medium septum, other divisions followed, the end cells being the largest and those in which the final septation takes place. Werner (1927) found that spore production varied in different lichens; in *Xanthoria* they were formed all the year round; mature spores germinated one or two days after ejaculation. A new feature observed by Werner in his cultures of lichen hyphae was the growth of conidiophores (aerial hyphae) which produced conidia at the tips, and these, scattered over the culture, formed the characteristic initials of thalline growth. This conidial reproduction was observed in cultures of several genera.

Physiology.

Water. In his studies of tropical lichens, Goebel (1926, 1, 2) tackled the problem of water supply. Intake of water, he found, was aided by the capillarity of hyphal hairs projecting from the margins or surface of the thallus or by cilia as in *Anaptychia*. In fruticose species such as *Usnea* water is imbibed over the whole surface, the amount absorbed through and up the central strand is negligible; this was tested by colour solutions in which the lichen was placed: the rise of water in two days was only 2 mm. In lichens generally water is taken in by the outer membranes and stored in these as well as in the central tissues. A distinction is drawn between mucilaginous hyphae (Quell-hyphen), mostly in the cortical tissue, sometimes in the medulla, and air-hyphae (Luft-hyphen), those that retain air in their net-work of hyphal strands, their dryness being secured by the presence of acids.

As to the amount of possible absorption, Goebel immersed *Cetraria nivalis* in water and it increased in 19 hours from 13·17 gm. in weight to 56·5 gm. The importance of water content was observed by Porter and Woollett (1929) during their work on seedlings where *Cladonia* "mats" occupied the soil, these

mats retained $4\frac{1}{2}$ times their weight of water before any passed into the soil, seriously affecting the growth of the seedlings by thus withholding the necessary moisture. Hilitzer's (1927) results as to water absorption and retention in his experiments are not entirely in accord with those of Goebel. Water, he found, was conserved in the cell-walls of the cortex, and not to any extent in the medullary tissues, and very little entered into the protoplasm. Absorption is highest in extended surfaces; isidiose and filamentous forms easily absorb from moist air. Stocker (1927), however, holds that merely moist air is insufficient, some degree of mist being required. Rapidity of evaporation varies; aerophil lichens, such as *Usnea*, dry quickly so that a humid atmosphere is essential to their healthy growth. Hilitzer finally concludes that the water economy of lichens is different from that of other plants, and that they are adapted to periodic drought. Joan Fraymouth (1928) proved that the amount of water present affected gaseous exchange which was specially slow in extreme degrees of drought, though vitality was not impaired, while respiration increased with the water content. She also found that the lichen gonidium was less favourably placed than free algae with regard to drought resistance.

Light and Shade. Lichens also vary in their requirements of light. Goebel (1926, 3) observed that in *Cladonia furcata* squamules were formed only on the side exposed to light. In *Peltigera aphthosa*, if algae alighted on the under side of the apothecia and became associated with the hyphae, the apothecium turned over to secure for them light exposure. Tobler (1927) found that Cladoniae were phototropic but only before the formation of the scyphus or head; also that other conditions, such as moisture, affected the direction of the podetium; the alighting of algae is important in this respect as they require light and influence the direction of growth. Stocker (1927) gave much attention to the problem of light: lichens are injured if exposed to strong light when they are fully saturated, as a too rapid evaporation is induced with a dry condition not favourable to assimilation. The maximum temperature for assimilation is much lower in rainy than in dryer areas; lichens with full exposure can flourish in a lower temperature than shade lichens. Large plants, such as *Lobaria pulmonaria*, a tree lichen often in the shade, must take advantage of every ray of sunlight. With full exposure direct sunlight is less necessary.

Colour. The subject of lichen coloration is closely associated with light and with air. Goebel (1926), in noting the green colour that follows moistening of the lichen, ascribes that to water entering air-containing cells—or, as in mucilaginous forms, the mucilage is rendered transparent by the inflow of water, grey-

ness being due to the presence of air. When acids give the tone of colour, the effect of light is very striking; the deepening of the colour in high light which induces increased acid production has often been noted—*Xanthoria parietina* growing in the shade loses the yellow colour. Tobler (1928), in discussing symbiosis, observes that the presence of acids and the colour induced by their presence is variable: in *Baeomyces roseus*, the rose colour of the apothecium is not constant and, occasionally, a sterile thallus may be tinged rose. Mattick (1929) repeats these statements in his consideration of Tauern lichens, the colour deepening to form a protection against too strong insolation. He noted also as an effect of light the tendency to narrow lobes and to panniform growth.

Cell-contents. Goebel (1926) observed as a consequence of algae alighting on the under surface of *Peltigera aphthosa* apothecia, that these not only turned to the light but the hyphae associated with the gonidia produced lichen acids. Schröder (1927) has called attention to the presence of calcium oxalate in species of *Porina*: it is not uncommon in lichens.

Bionomics.

Rock Disintegration. The relation between the lichen and the substratum has again been tested by E. J. Fry: this time with a series of saxicolous species; her results are correlated with her previous study of corticolous forms. She found the same agents—wetness and dryness—at work with alternate swelling and contracting of the hyphae causing an arching of the tissues, especially below the apothecia, with a dragging up of minute fragments of rock; similar disintegration was also noted at the edges of the thallus. Experiments with gelatin models of apothecia and thalli on the bare rock confirmed the theory that disintegration is mechanical. The action of acids produced by the lichen is thus, she considers, negligible, except in the case of limestone rocks, but even then the action is mainly mechanical.

Increase in Size. A number of observations confirm the slow growth of lichens. Mattick (1929) watched the progress made by the young thalli of several species from May to August: in that case careful measurements showed no calculable increase. *Xanthoria* and *Physcia* on a memorial stone were measured and had reached only 2–3 cm. in 12 years. Lange (1929) cut away part of a vigorously growing *Peltigera polydactyla* and 3 years later the space was entirely regrown. *P. spuria* was seen to increase till the third year when fructification took place, in the fourth year the lichen had disappeared. L. Porter (1927) also contributed notes on this subject: in 7 years a gooseberry bush had acquired a considerable colony of lichens on its better lighted

branches. Estimation as to the increase of *Parmelia caperata* gave approximately about 1 cm. per annum. Tengwall (1928) took notes on growth rate during a period of 5 years, and calculated that *Cladonia alpestris* would require 30 to 45 years to attain 60 mm. in height, *C. rangiferina* reaching the same height in 15 to 20, and *C. sylvatica* in 20 to 30 years. *C. uncialis* grew quickly, while *Stereocaulon* reached its maximum of 50 mm. in 15 years. A lichen sward, he judges, would require 15 to 30 years for regeneration. *Stereocaulon* may be reckoned a pioneer in colonisation, but it pushes out other Cladoniaceae.

Phylogeny.

W. Watson (1929) has worked out a comprehensive scheme of classification on phylogenetic lines—the presumed development of lichens from their origin as symbiotic organisms. He recognises *Biatora* and *Lecidea* as the base of the Discolichenes, developing to Lecanoraceae or to Lecideaceae with advance, especially in the former, to the larger lichens. Spores—their septation and colour—mark recurrent lines of advance or of deviation, and opinions differ as to whether a genus like *Physcia* with two-celled brown spores be not developed from Lecanoraceae. Watson, however, makes *Buellia* the base of a *Physcia* phylum, and, with *Buellia*, he connects *Rhizocarpon*. There is strong resemblance certainly, but they also have much in common—in the formation of the apothecium—with Lecideaceae. There must be divergence of views, and this expression of opinion is welcome and helpful. Watson has suggested alterations in the grouping of orders and has also made some changes in generic status.

Two papers by Elenkin (1929) on the classification of lichens have a direct bearing on phylogeny. He has sought to tabulate in formulae the precise value of the characters in each symbiont that have influenced development in this new plant type. Both organisms had already reached a certain status: the fungus had evolved its fruiting form before the combination, the alga was more pliable and more in abeyance. There follows his pronouncement that the vegetative thallus is a product of new conditions—"a homogeneous mycelium under the influence of symbiosis with algae, and the direct action of the air has established the essential growth types." To return to a more familiar statement, the algae require light and air for photo-synthesis, hence the variety of form which has become established to secure the best conditions for the formation of essential carbohydrates.

The phylogenetic development of the podetium in *Cladonia* has again been a subject of study and of controversy. M. and

Mme Moreau (1927 and 1928) trace its origin to cortical cells and compare it with the origin of isidia in *Parmelia scortea**. They thus reject Wainio's generally accepted view of the podetium, as a secondary structure reproductive in origin. Choisy (1927) has given his opinion in favour of the reproductive hypothesis, and, as proof, points out that the gonidia take no part in the early stages as they do in the growth of isidia: they are late arrivals on the developing organ, and remain on the periphery, thus resembling the development of *Bacomyces*. The Moreaus having repeated their conclusions (1928); Choisy (1929) has again pointed out that the structure of the podetium is on the same lines as the lecanorine enveloping apothecial margin, which includes gonidia, and he cites the fact that the gonidial layer in the thallus is interrupted by the emergence of the more deeply seated podetium, a development radically different from that of isidial papillae of superficial origin. The controversy must be judged on morphological grounds, and there seems little doubt that the podetium originated as an organ of fructification, though later it assumed the function of an assimilating thallus.

Choisy (1928) has further propounded a scheme of phylogeny in Cladoniaceae, with a classification that gives considerable importance to the "spermogonia." The interpretation of these bodies now accepted by most lichenologists is that they correspond to the pycnidia of Ascomycetes, and are, therefore, subsidiary organs. It is evident that a phylogenetic classification must primarily be based on the perfect fruiting condition as in other plants.

Systematy.

Classification. One of the most important works on this subject is Vainio's *Lichens of Finnland*, Part III, which deals with Coniocarpineae (1927). The whole group is distinguished by a thallus which may be reduced to non-existence. Most of the genera and species, however, are distinctly symbiotic plants—a few only have reverted to saprophytism. Vainio has accepted the view that these latter are true fungi; he has created, for instance, the fungal genus *Calicella* for two such species hitherto ranked in *Calicium*, and he has established several new fungal genera for the reception of other questionable species. More intimate knowledge of fungi†, as well as of lichens, might clear the debatable ground.

A study of Moriolaceae has been carried out by Bachmann (1926). The family with two genera, *Moriola* and *Spheconisca*, was first described by Norman. In the present study of this obscure group of plants Bachmann has determined the algal

* See p. 200. † See p. 197.

symbionts to be Cyanophyceae which occur in groups to which Norman had given the name "goniocysts." The genera *Moriola* and *Spheconisca* are retained, but a number of Norman's species are rejected as being fungal. In a later study Keissler (1927) decides that all of the forms are fungi with the possible exception of one species of *Spheconisca*. There has also been published a *Synopsis of Stereocaulon* by Carroll W. Dodge (1929). Along with a synoptic key he has given an account of all recorded species with many critical and explanatory notes. Dodge has followed Lincoln Riddle in making use of the cephalodia as a good diagnostic character, not only their form and occurrence but the type of alga present in them. Hillmann (1930) has studied the family Teloschistaceae. He includes species with bipolarilocular spores (*Euteloschistes*) and also those with three septa (*Niorma*). He discusses sympathetically Hue's view of the one-celled nature of the bipolar spores. He suggests that *Physcia megara* and *Chlorea flexuosa*, with more exact knowledge, may yet be included in Teloschistaceae. Schilling (1927) has rearranged the plants included under the tropical epiphyllous Strigulaceae. He has treated the subject under various aspects—the identification of the alga, the relation between the symbionts and the varying growth on the leaves as well as the development of the apothecia. In some instances the supposed lichens were proved to be parasitic fungi. The gonidia are mostly species of *Phycopeltis* or of *Trentepohlia*, though the alga, he decides, is not all-important in his view of classification. He adds a new genus, *Coniscocaulon*, with *Pleurococcus* gonidia.

Magnusson's *Monograph of Acarospora* (1929) is a valuable contribution to lichen literature. It is the fruit of long study, worthy of high distinction, and can be classed for completeness with Vainio's Cladoniae. He lists 199 species from all over the world, with full descriptions, and citations, and with not only locality but the particular habitat. The work is prefaced by a general account of the genus—thallus, fructification, etc., by notes on the ecology and by a comparative reckoning of the species found in the different countries. Many of the species have been determined by Magnusson himself; he has examined most of the authentic types and rewritten or rather considerably enlarged the descriptions. It is impossible to overestimate the value of this compilation.

We have also to record Hansen and Lund's *Danish Cladoniae* (1929). A short account of the genus is given followed by descriptions (in Danish) of all the species found in Denmark. The work is well provided with keys to the species. They have not listed *Cladonia mitis* as a distinct species. It differs from *C. sylvatica* mainly in the taste which is altogether mild. They quote

Vainio's view that it is the union of characters that must decide the species in *Cladonia*.

Malme's studies of S. American genera collected under the auspices of the Regnell Expedition are also of general importance. In one of these on the Buelliae (1927) he states that he found the genus well represented in all the different regions—on the Rio de Janeiro, Matto Grosso, Paraguay and north of Rio Grande do Sul. The record comprises 47 species, many new to science. He found that spores became darker with age and that the thickness of the central septum tended to disappear; "possibly being used as reserve nutrition by the developing spore." A key is provided for the species which are fully described in the text.

In two other papers (1928 and 1929) he deals with the Pyrenocarpeae; in the first with genera that have few representatives. He found considerable distinction between the forms found in the different states from tropical to subtropical. Research by cultures is, he considers, advisable to distinguish with accuracy the different gonidia which—especially in *Trentepohlia*—break up within the thallus. A new genus, *Porinopsis*, is described. The second publication deals with *Pyrenula* and *Anthracothecium*, both abundantly represented in the tropics. In *Anthracothecium* the spores had frequently a clear mucilaginous wall (halonate), evidently, he decides, of service in dispersal as they are thus able to adhere to leaves, insects, etc.; they also contained oil drops.

A puzzle in Systematy has been partly solved by Thaxter in his notes on a leaf lichen, *Myxotheca hypocreoides*, at one time classified as a fungus. The plant forms whitish cushions on a subiculum, the fringe of which is associated with *Trentepohlia* sp. The cushions are packed with large thick-walled asci; as the ascus develops, it gradually presses outward the surrounding matrix of granules, and the fine disorganised hyphae which form one envelope about it. The surface of the cushion or stroma is formed by branching and anastomosing "paraphyses." A similar plant from Borneo was described by Krempelhuber as a new lichen genus and species, *Myriostigma candidum*. Vainio next classified it as *Arthonia* (*Arthothelium*) *candidum*. Still another name was given to a specimen from Jamaica, *Ascomycetella filicina* Ellis & Everh. It is probable that there may be a specific distinction between the American and the Asian plant, and Thaxter has also suggested a resemblance to the genus *Cryptothecia*, but with very marked differences. The isolated asci recall that genus but in *Cryptothecia* the "stroma" in which they are embedded has a thalline structure with definite gonidial zone, whereas in *Myxotheca* a hymenium is present.

Ecology.

Associations. A number of important papers on this aspect of lichen study have appeared within the last few years. In a general discussion Du Rietz (1925) points out that though there may appear to be no chemical difference between one substratum and another, the plants exhibit a selective quality which lies at the base of association.

In the extreme north Harshberger (1928) found that societies in the Alaskan tundra were largely composed of one species—*Cladonia rangiferina*, which was there the most important lichen. In south Norway Du Rietz (1925) found two types of vegetation: on the higher ground above 1100 m. the principal lichens were *Cetraria cucullata*, *C. islandica* and *C. nivalis* with Cladoniae and Gyrophorae, though many others, as well as phanerogams, formed part of the associations. The lower ground was occupied by dwarf shrubs, grass and heath; the dominant lichens there were *Cetraria nivalis* and *Alectoria ochroleuca*.

Further south in the Moraine district of Schleswig, Erichsen (1928–30) has described in great detail the associations of lichens down to the Holstein border. On the eastern side the soil is glacial, composed of clay and chalk. A line of dry mounds lies to the west, on the further side of which there is a sandy region of moors and heath, with here and there projecting rocks. Erichsen collected 450 different species, nine of them new to science. The climatic conditions are Atlantic—moderate temperature, heavy rainfall with great moisture and high westerly winds. Erichsen groups the lichens under the three areas—the strand or maritime zone, the Moraine district and the western sand territory. In the first, maritime associations predominate; the moraine proper is highly cultivated and lichens, mostly on trees and buildings, were generally scarce. On erratic blocks, on heaths and moors, he found many glacial species such as *Cetraria islandica*, *Gyrophora polyphylla*, *Lecanora badia*, etc. He also noted the influence of the wind in the crumpled proliferous growths, with the thickening of the cortex. In another paper (1928) he gives the lichen flora of an inland sand dune (Süderlügum) mostly covered with *Calluna* plants. Cladoniae were abundant; *C. sylvatica* by its vigorous growth even crowding out the heather plants. Among pioneers he includes *Lecidea uliginosa* which has also been noted as a pioneer on the sand dunes at Alberta, Canada.

Anders has made a study of the lichen flora of the Kummergebirge in north Bohemia. He gives a series of associations according to substratum: soil, grassland, bark, wood and rock, with a further series designated by him as "parasites" which

grow over other lichens or mosses. The rock lichens were by far the most abundant—the rarest species on silicious rocks were *Placodium Garovagli* and *Parmelia Mougeotii*; on the calcareous substratum *Toninia coeruleo-nigricans* with some others appeared as dark patches on the white limestone. Anders noted with great appreciation the stately growth of *Cladonia alpestris* var. *sphagnoides* "standing solitary among a proletariat of crustaceous forms." This variety has been found only in Bohemia. On the serpentine soil of west Bohemia, Suza determined two distinct associations: the terrestrial and the epilithic. In the former, lichens were mingled with the heaths; in the latter, on the serpentine rocks, they were subject to great dryness, and common species, such as *Rhizocarpon geographicum, Lecanora glaucoma, Diploschistes scruposus*, etc., were absent as also a *Gyrophora* species which grew freely on the neighbouring schists. No true lime lichens were to be found, but birds supplied the material for a nitrophilous association.

Hilitzer (1927) determined fifteen different associations on the lydites of Czecho-Slovakia, each marked by some dominant species. A calcicole association was discovered on an old building, and nitrophilous lichens flourished on the resting places of birds. On the more purely lydite rocks he noted *Pertusaria lactea, P. corallina, Gyrophora polyphylla* and *Parmelia Mougeotii* as the most characteristic species. In another paper (1927) he gives an account of the lichen flora on the eastern Sudetes. He found two northern species, *Thelopsis melathelia* and *Parmelia infumata*, which he pronounced to be relics of glacial times.

Podpěra (1928), in an ecological survey of the Pollauer Berge in Moravia, includes a series of calcicolous lichen associations on the limestone, rather scanty, however, as there are few exposed rock faces and they almost exclusively consisted of crustaceous forms. Silicicolous lichens were found on bridges and buildings in the valleys. Domin (1928), in the same region of the Tatra Mountain, studied plants from an edaphic standpoint. The lichens were mainly calcicolous but layers of humus formed a nidus for some of the larger forms (Cetrariae, Cladoniae, etc.); the forest lands yielded still other types, while a granite mountain displayed Rhizocarponetum and Gyrophoretum associations.

Magnusson has included ecological conditions in his *Monograph of Acarospora* (1929). Most of the species are saxicolous, a certain small number are lignicolous, and a few others are terricolous. They are as a rule particular as to the composition of the substratum: some grow only on sandstone, others on volcanic rocks; a rather large number grow only on calcareous rocks or earth. Most species are nitrophilous. An interesting

group are those that settle on other lichens and gradually destroy them.

Cengia-Sambo's paper on "Lichens as indicators of climate" has a particular bearing on ecology. She has examined and correlated lichens from many regions beginning with northern Patagonia, Chubut and Argentina, and finds that though lichens are ubiquitous certain types are peculiar to certain climatic conditions. She finally summarises the different types as (1) desert stony, polar, (2) tundra stony, (3) cold temperate zone, (4) temperate zone, (5) tropical and (6) subtropical. Mountain lichens correspond with those of high latitudes: those found above 2400 m. being of polar type or snow lichens.

Specialised Associations. Epiphytes. This association includes lichens that grow by preference or of necessity on other plants. The most noteworthy are the leaf lichens so abundant in the tropics though rare and not always obligate in temperate regions. Ochsner (1928) in his inclusive paper on epiphytes finds lichens the most important members: of the 280 species dealt with 130 were obligate. The conditions influencing their occurrence are the kind of bark, orientation and altitude which entail the decisive factors of light, temperature and moisture. Ochsner listed the trees with the lichens on each and the special associations formed. Thus a *Lecanora subfusca* association included as important members *Lecanora sufusca*, with its close allies, *Lecidea parasema, Pertusaria communis, Phlyctis argena* and *Ph. agelaea*. He gives also observations on altitude and succession. An *Usnactum barbatum* association grew best at 1000–1500 m. Maria Cengia-Sambo (1928, 1929) has given a similar paper on the ecology of corticolous lichens: she emphasises the influence of the type of bark rather than the kind of tree, as a variation of bark on the same tree accounts for different lichens. Humidity, due to habitat and atmosphere, are also controlling factors; some few species are limited to special trees such as pines. The prevailing climate and the kind of substratum also come into play: thus epiphyllous species are rare in temperate climes where the leaves are deciduous, though abundant on evergreen trees in the tropics. Many species are more or less adaptable: *Parmelia acetabulum* and others change from trees to rocks. *Parmelia saxatilis* which is saxicolous in Italy becomes corticolous in St Helena. Nikolsky (1928) has specialised on epiphytes in his *Lichen Formations* in a pine forest on sandy ground in north-east Russia; he deals with 77 species—the largest number were in the Pinetum-Cladinosum group, the most frequent species, *Evernia thamnodes* and *Parmelia physodes*; the most selective, *Anaptychia speciosa* restricted to the few trees of *Populus tremula*, and *Physcia stellaris* which grew only on *Pinus sylvestris*.

The lichens of apple trees in West England are described by Stuart Light: with regard to their position on the trees, *Parmelia caperata* was mostly on the upper reaches, *Xanthoria parietina* about the middle and *Evernia prunastri* all over. A somewhat similar study by the Moreaus (1926) deals with a beech forest (Puy de Dome), a uniform locality with trees of various age, mostly beech. The authors note the preferences of the lichens for certain trees and their position on them; only a limited number grew on smooth young bark, or in the shade. *Evernia prunastri*, *E. furfuracea* and *Ramalina farinacea* were rarely absent from the older trees. *Parmelia sulcata* was constant and abundant. *Parmelia saxatilis* favoured the base of the trees, probably owing to a greater moisture there; the authors also observe that in the shade, where assimilation was difficult, the lichens probably depended to some extent on the substratum for carbohydrates.

Zahlbruckner, Keissler and Allan (1928) have described the epiphyllous lichens of Kitchener Park, New Zealand, and have also described the type of leaves on which they grow. The most common species was *Lopadium subcoerulescens* which was found on the leaves of thirty-one different trees. Zahlbruckner determined a number of new species, and Keissler a new parasite that grew on the *Lopadium*, possibly a stage of the fungus *Cyphella aeruginascens*. Paul van Oye (1924) compares the epiphyllous lichens in the Belgian Congo with those of Java. There as in other tropical lands those associated with *Trentepohlia* were numerous. Schilling (1927) in his account of epiphyllous lichens in Java confines his attention to the systematy of Strigulaceae. Plitt (1929) has revived an old interest in his examination of those that grow on drug-producing trees such as *Cascara Sagrada*, *Cinchona* and other "officinal" trees. The best known study of "officinal" lichens is that of Fée (1824); the object then was to find if the lichens on the tree affected the quality of the drug. Plitt's study has a wider range of outlook and of material: he found that certain lichens favoured certain trees as, for instance, *Thelotrema lepadinum* which was always found on the trunk of *Cascara*. The question now is how much the tree—type of bark, exposure, etc.—influences the kind of lichen growth. Crustaceous species were the most abundant.

Distribution. Floristic Lichenology—a specific study of lichen plants with their occurrence and habitats—is of the first importance. Many of the papers published have dealt with the distribution of particular plants or families. Such a paper is that of Darbishire (1928) who has traced the occurrence of Roccellaceae in both hemispheres. The species are limited in number; all inhabit somewhat warm climates and are mostly maritime; the influence of temperature has been shown by the use of isotherms.

Three new species of *Roccella* have been described from Zanzibar and Madagascar by Choisy (1929), all of them grew on trees and are distinguished more or less by the tendency to yellow colouring.

Garside (1929) has traced the boundaries of *Siphula*. The genus contains fourteen species, three of which occur in S. Africa. One species is fairly common in Scandinavia. Arwidsson (1926) described *Siphula ceratites* as arctic and circumpolar, alpine in character, but found also at sea-level.

Du Rietz (1926) in his study of *Evernia*, *Letharia* and *Usnea* allows only two species of *Letharia*, *L. vulpina* and the closely related *L. californica*; other species are included under *Usnea*: the character of the central axis is the determining feature and that—as many have found—is often problematic. His view has much to justify it, but we would need a special section of Usneae to simplify matters. *Usnea sulphurea* has long been considered a bipolar species. Du Rietz finds difference enough to limit the true *U. sulphurea* to the Arctic, and classifies the Antarctic forms as *U. Taylori* and *U. aurantiacoatra*, the latter species very common in S. Georgia. There remains the fact that both "species" are astonishingly alike.

In a further paper (1928) he clears up the ambiguity as to distribution between *Gyrophora anthracina* and *G. rigida*, the latter plant being Scandinavian, and one of the West Arctic group of plants common to Scandinavia and N. America. He considers that *G. rigida* must have survived the glacial period "on any wind-exposed rock rising above the ice-cover." Bernt Lynge refers also to these ancient days in his *Lichens of Novaya Zemlya* (1928), where he collected some 7000 specimens. He argues from his studies of 413 different species—from the lowlands and talus slopes—that Nova Zembla had been immersed in the sea during a first glacial period, so that all the lichens come under the term "recent." The paper abounds in notes on climatic and other influences. Zahlbruckner (1928) took charge for him of the genus *Lecanora*; Magnusson (1928) of *Acarospora*. Magnusson (1927–29) has further enriched lichen literature with papers on new or interesting species for Sweden and North Russia, while Lynge (1929), on stones brought by geologists from the Taimir peninsula (N. Siberia), has determined 45 Arctic species, many extremely reduced as to thallus, the commonest *Rhizocarpon geographicum* and *Gyrophora proboscidea*. Oxner (1929) gives an account of the Kamtschatka lichen *Ramalina Rjabuschinskii* found by Savicz but considered by Du Rietz to be a synonym of *R. Almquistii*. Oxner finds that the two are distinct differing in the character of the central tissue. In another paper (1929) he lists the tundra lichens of the peninsula Tschuktschen, in extreme north-east Asia. Among others found

were *Siphula ceratites*; *Cetraria Kamezatica* previously found in Kamtschatka was also collected there. Paulson in his *Spitsbergen Lichens* (1928) includes notes on the influence of Arctic conditions on the plants, and in *Lichens from Yunnan* (1928), the Alps of Chinese Tibet, he found that most of the species from these high altitudes—3,000–16,000 ft. were also alpine in character.

An immense number of lichens has been recorded from many countries. It is possible in the space at command to indicate only the scope of the work done. The reader is referred to the list of literature for the full record. Our knowledge of lichens and their distribution owes much to these papers. One of the most important is "The Lichens of Ireland" by Matilda C. Knowles (1929). The territory has been divided into forty topographical divisions and a number of botanists took part in the survey, every plant being tested or determined by M. Knowles herself. A considerable number are recorded from Ireland that have not yet been found in Great Britain. Alpine species are rare; subalpine are abundant, and a number of tropical or subtropical species grow in the south-west. The work is claimed by the author to be only a starting-point for further exploration. Papers on distribution in Great Britain include the account by Knight (1928) of lichens collected during the forays of the Mycological Society at Marlborough (Savernake Forest) in spring and in the Highlands of Scotland (Aviemore) in autumn in which district rock specimens and alpine forms were conspicuous. Knight (1928) has also given species collected in S. England, while Paulson (1929) lists those found in the Oxford district. Watson has carried out for years an examination of Somerset lichens, and the completed list has appeared lately (1930). He gives in the introduction a historical account of lichens in the county and follows with his own list of over 500 species, with many varieties and forms. In no other county has such a fine record been given. We have also to acknowledge the "Lichenological Notes" published by Watson (1928, 1929) in which he has recorded new species and new records for Somerset and for Great Britain. Several species recorded only for Ireland have been found by him in Somerset.

On the Continent much floristic work has been done. Erichsen (1928, 1929) in an ecological paper gives the lichen flora of Schleswig Holstein. Cypers-Landrecy (1926) has been working in Bohemia. Lange (1929) collected over the Erzgebirge partly in Saxony and partly in Bohemia—a varied territory of valleys and woodland, with hills up to 1244 m. in height. The locality is described and the changes that have interfered with lichen growth. The exposed rock faces were covered with crustaceous species but where limestone was present, blasting operations had

destroyed the flora. Pine forests had replaced beech and other woods, and, in other places, advancing woodland had brought too much shade. In his notes he states that *Parmelia conspersa* fruited well and that *Cetraria islandica*, abundant over the whole district, was densely sorediate on the upper surface—an unusual condition.

Fran Kušan (1928) in Poland, and Suza (1928) in Jugoslavia have contributed largely to the knowledge of lichens in their territories. Szatala (1927) has issued the first instalment (250 species) of a lichen-flora of Hungary; Fóriss (1928) has contributed many records and Gyelnik (1926–18) has written critically also on Hungarian lichens, as Nikoloff (1928) has done for Bulgaria. Oxner (1927 and 1928) has been working on lichens in the Russian Ukraine and Tomin in south-east Russia—all these papers of great importance as regards lichen distribution.

Detailed work is contributed by Anders (1928) in his examination of the Kummergebirge, an isolated arenaceous plateau in North Bohemia up to 773 m. high. The various geological features are explained: on the uplands the region is dry, but there is abundance of moisture in the lower reaches. Lichens on the different substrata are listed—on soil, meadow, trees, wood and stone (sand and lime). Finally, a list of fungal parasites is added. Mattick (1929) has chosen the Nature Reserve—the Tauern Park—for exploration. The lichens of each locality are given on trees—solitary or in woods—on the ground, on stones, etc., and special attention is given to those of the higher altitudes: crustaceous species reach the highest rocks bare of snow, and the most inaccessible crags are adorned with green or red patches of *Rhizocarpon* or *Caloplaca*. Mattick compares his results with those of Anders in the other sections of the Tauern. Servit in his "Lichens of Jugoslavia" (1929) has concentrated on the Velebitgebirge which rises from the Dalmatian coast to a height of 1610 m. opposite the Island of Arbe. It is a locality peculiarly favourable for lichens, owing to abundance of sunlight and moisture, in a region of sea coast and forests. He divided the territory from the shore inward and upward into fifteen distinct territories, with the lichen-flora of each. Diagnoses of new or doubtful species are given. New ground has been broken by Bornmüller (1929) by his collection and list of lichens in Macedonia—also a valuable addition to distribution.

In Switzerland Frey (1929) is continually adding to the lichen-flora, and finding new species and new genera. Further south there have been extensive collections of Collemaceae by de Crozals (1927) at Toulon; Maheu and Gillet (1926) have issued a list of Corsican lichens collected by Mme Gillet and by Zschacke just before the war; and Zschacke himself (1927) has published a

further list. Maheu and Gillet have also given an account of lichens in the Balearic Isles (1921) and in N. Africa (1925). Many new species are described in the various papers.

Mameli-Calvino and Agostini (1929) have added many species to the lichen-flora of Forlivese, a district that includes the pine woods of Ravenna, and various river valleys on the Adriatic coast. Maria Cengia-Sambo has noted in her study of "Lichens from the Island of Rhodes" (1927) that they were typically eastern Mediterranean and resembled more closely the lichens of Asia Minor than those of Greece, the reason probably being that "Rhodes formed part of the mainland in the Miocene and Pliocene eras." She has also worked out the lichens in "Chiovando's Flora of Somaliland" (1929). The most numerous were Graphideae growing on the phanerogams of the collection, and desert forms, one a blue-green mucilaginous species. Brno Schröder (1927) has listed the 73 lichens collected by him in East Africa that had been determined by Zahlbruckner in 1926.

From the Far East we have to record Du Rietz's work (1929) on the lichens collected in Kamtschatka by E. Hulten, the botanist of the Swedish Expedition (1920–22); a number of familiar as well as of new species are added to the flora of that country, and the writer has added many critical notes. Many new species are included among the 208 listed for Japan by A. Zahlbruckner (1927) and the same indefatigable systematist (1928) has published new or insufficiently described lichens from Java, with one new genus, *Bogoriella*, allied to *Microthelia*. Harmand too, before his death, had prepared a paper on lichens from China with a few from Singapore—82 species, a considerable number new to science. Paulson's lichens from Yunnan (1928) collected among the Alps of Chinese Tibet by J. W. and C. J. Gregory have already been referred to.

In the Western Hemisphere a series of lichens collected by Macoun in 1907 have finally been reviewed and published by Dodge (1926). He notes that Cladoniaceae were the most numerous in the collection and these have been accorded special attention. Cladoniae also were the main items in the collection of forage plants from Alaska determined by Merrill (1929). C. A. Robbins (1927 and 1929) has also done discriminating work on this difficult genus.

Lichens recorded from the Gaspé Peninsula, Quebec, have been summarised by Dodge, especially Cladoniae. Lists of the "Lichens of Connecticut" have been published by A. W. Evans and Rose Meyrowitz (1926), and by Evans alone (1927). They tabulate all the lichens collected by various botanists. The number amounts to 301 species; they acknowledge much assistance given by ecologists. Magnusson (1929) contributed to

Mycologia a paper on the yellow species of American Acarosporae, which are now included in his monograph.

The cryptogams of Porto Rico have been much studied of late: Professor Fink, before his lamented death, had collected there and had prepared a paper on Graphideae (1927), all of them new to science. Zahlbruckner has taken up his task and in a first paper (1930) describes 27 species new to science, belonging to many different genera and all crustaceous with two exceptions, *Usnea Finkii* and *Ramalina Finkii*. Vainio (1929) also had had a series submitted to him by Fink, among them he found two new genera, *Finkia* and *Gyrocollema*, both crustaceous and with blue-green gonidia, the latter with lecideine apothecia. Lichens collected by G. Bues in Peru were determined by Merrill (1927) who also has recently passed away.

Succession. Associations tend to change to some extent as the more vigorous lichens supplant those of slower growth. Menzies (1926–27) traced the succession on a patch of burnt soil in Perthshire. The first coloniser was a species, not determined, with small foliaceous fronds but no fructification. It was followed and dispossessed the following summer by *Peltigera spuria* a lichen not seen previously in the locality. Mattick (1929) in the Tauern Park observed that Lecideae, Lecanorae and Pertusariae were the first to appear on the smooth bark of young trees, followed later by the larger Parmeliae, Cetrariae and Usneae.

An interesting discussion as to succession in lichens has been published by C. Plitt (1927) based on observations made in Jamaica. On rocks in pine woods crustaceous forms were—as elsewhere—the first colonisers. Later when pine needles fell *Cladonia rangiferina* became prominent and if bits of wood were present *C. cristatella* made its appearance. *Parmelia conspersa* also arrived but grew only in full sunlight. As a rule crustaceous species were supplanted by the foliose, but *Parmelia* was checked by *Lecanora gibbosa*, which in turn was overgrown by *Candelaria concolor*. In one locality he noted a struggle between *Parmelia* sp. and *Sticta* sp. The latter had a thallus with raised margins and was thus able to grow over and finally evict the *Parmelia*. In general, Plitt found that crustaceous species developed first, then followed foliose forms among which there was keen competition for place. Fruticose species in turn may oust the foliose. *Usnea* species invading a tree trunk frequently crowd out all other lichens.

A typical epiphytic succession was traced by Ochsner (1928) in Switzerland. The association began with *Phlyctis argena* and *Graphis scripta*, later arrived *Lobaria pulmonaria* and formed a purely *Lobarietum pulmonariae*. Mattick (1929) in the Tauern Park found that crustaceous species of *Lecidea*, *Lecanora* and

Pertusaria were the first colonisers on the smooth bark of young trees; they were followed later by larger forms—Parmeliae, Cetrariae, Usneae, etc.

Economic and Technical.

Harmful Lichens. Ochsner (1928) in his study of epiphytes found that lichens on trees might induce conditions of moisture which encouraged the growth of fungi and bacteria, and that these might injure the tree by penetrating the living tissues. Schilling (1928) made similar observations. A different interpretation of the harm done is reported by Philipps from S. Africa. He noted that *Usnea* spp. grew freely on trees especially on *Podocarpus* and also the condition of the trees, the sickly appearance and the degeneration of the buds and young shoots evidently due to the epiphytes, and he attributed the harmful influence to parasitism, though almost certainly the effect was the mechanical smothering of trunk and branches. Lichens are not difficult to kill off: a coat of whitewash would relieve the trees. Ryosi Arnó (1925) in another connection found that water charged with sulphur dioxide and directed over lichens induced a too great acidity and destroyed the plants: lichens in general suffer from acid in water more than the higher plants.

Lichens as Food. In a paper on the vegetation of Central Alaska, the late Professor Harshberger (1928) wrote on the importance of utilising the "barren grounds" or tundra in the raising of caribou for markets. The caribou feeds on the reindeer lichen (*Cl. rangiferina*) as well as other tundra plants and in winter it uses its paws and antlers to scrape away the snow and get at the underlying plants. L. J. Palmer was also on the same quest in Alaska investigating the habits of the reindeer. He collected all the possible forage plants among which lichens bulked largely. They were submitted to G. K. Merrill (1929) who determined 67 different species, but these could not all have been food plants.

Interesting data are given by Günther Schmid (1929) on the lichens that serve as food for snails. He watched the behaviour of two small species, *Chondrina avenacea* and *Pyramidula rupestris*, as they travelled back and forth over a limestone rock grey with crustaceous lichens such as *Verrucaria calciseda* and *Protoblastenia rupestris*. The hyphae of limestone-penetrating lichens develop oil and it was concluded that the snails were specially attracted by the rich material. No traces of the hyphal fat cells were found in their excrements, so probably they were entirely digested.

Experiments on Dyeing. Not much has been recorded in regard to dye-stuffs. One paper only is of interest—that of Selim

Augusti (1928). By experimenting with *Cetraria islandica* he procured a faint yellow colouring matter which he found of value in dyeing suede as it gave the faint pastel tints so much sought after in gloves.

LIST OF PUBLISHED LITERATURE.

Abbayes, Henry des. Note sur le *Lecidea* (s.g. *Bilimbia*) *Corisopitensis* Picq. Bull. Soc. Sci. Nat. Ouest France, III, pp. 74–7, 12 figs. (1923).

—— Lichens récoltés en Loire-Inférieure et dans quelques localités de Vendée et Maine-et-Loire. Op. cit. IV, pp. 31–139 (1924).
A list of 139 species collected and determined by Abbayes.

Ádám, Boros. Grundzüge der Flora der linken Drauebene mit besonderer Berücksichtigung der Moore. (Lichenes, p. 20.) Magy. Bot. Lapok, XXIII, pp. 1–71 (1924).
A general ecological paper with some reference to lichens.

Anders, Jos. Untersuchung über *Mycoblastus sanguinarius* (L.) Norm., *M. alpinus* (Fr.) Kernst. und *M. melinus* (Krplh.) Hellb. Hedwigia, LXVIII, pp. 87–92 (1928).
Anders after examination of many specimens has decided that there is only one species, *M. sanguinarius*, and that the other two are varieties; all have the blood-red colour at the base of the apothecium.

—— Die Strauch und Laubflechten Mitteleuropas. Anleitung zum Bestimmen der in Mitteleuropa vorkommenden Strauch- und Laubflechten, pp. 1–217, 30 pls. 8 text-figs. Gust. Fischer (1928). See Hedwigia, LXVIII, Beibl. pp. 69–70 (1928).

—— Die Flechtenflora des Kummergebirges in Nordböhmen. Lotos, LXXVI, pp. 315–25 (1928).

Andrews, F. M. A Study of Lichens. Proc. Indiana Acad. Sci. XXXVII, pp. 329–30 (1928).
A note on the influence of environment on the occurrence of lichens, as, for instance, smoke of towns and undue moisture, etc.

Arnó, Ryosi. Contribution to the Physiology of Lichens. Japanese, with plant names in Roman characters. Bot. Mag. Tokyo, XXXIX, pp. 361–80, 1 fig. (1925).

Arwidsson, Th. Die Verbreitung von *Siphula ceratites* (Wg.) E. Fr. anlässlich der Auffindung der Art in Schweden. Bot. Not. pp. 379–92, 2 maps (1926).
Siphula ceratites is fairly abundant round the subpolar coasts. It has also been found in America.

Augusti, Selim. Ricerche sperimentali sul Lichene Islandico e sulle sue possibili applicazioni in tintoria. Bol. Soc. Nat. Napoli, XXXIX, pp. 207–10 (1928).

Bachmann, E. Hexenbesenbildung bei einer Strauchflechte. Hedwigia, LXVI, pp. 331–6, 3 figs. (1926).

—— Die Moriolaceen. Nyt Mag. Naturvidensk. LXIV, pp. 172–288, 3 pls. 13 figs. (1926).

—— Zur Gonidienvermehrung bei Flechten. Ber. Deutsch. Bot. Ges. XLV, pp. 308–14, 2 figs. (1927).

—— Die Beziehungen der Knochenflechten zu ihrer Unterlage. Ber. Deutsch. Bot. Ges. XLVI, pp. 291–7, 1 fig. (1928).
The lichen *Verrucaria* sp. forms a dark thallus on the surface of the bone and is not endolithic: lichen hyphae do not dissolve bone material.

—— Nochmals *Stereocladium tirolense* Nyl. Hedwigia, LXVII, pp. 99–109, 7 figs. (1927).
Further collections of the lichen determined as *Stereocaulon tirolense* by Bachmann have decided him to make another species *S. saxonicum*. It is distinguished by phyllocladia, spore-septation, etc.

Bachmann, E. Der Thallus der deutschen Sarcogynearten. Tom. cit. pp. 131–40, 1 pl.

—— Hexenbesenbildung bei *Cladonia amaurocraea* (Flrk.) Schaer. Op. cit. lxviii, pp. 5–10, 6 figs. (1928).

—— Die deutschen felsbewohnenden *Segastria*species. Op. cit. lxix, pp. 287–300, 9 figs. (1929).

—— Der Lagerbau bei *Verrucaria*. Ber. Deutsch. Bot. Ges. xlvii, pp. 554–60, 1 fig. (1929, 2).

—— Die Pilzgallen einiger Cladonien. Archiv Protistenk. lvii, pp. 58–84, 10 figs. (1927).

—— Das Verhältnis flechtenbewohnender Pilze zu ihren Wirtspflanzen. Op. cit. lviii, pp. 151–2 (1927).

—— Die Pilzgallen einiger Cladonien. III. Op. cit. lxii, pp. 261–306, 52 figs. (1928).

—— Die Pilzgallen einiger Cladonien. IV. Op. cit. lxiv, pp. 109–51, 44 figs. (1928, 2).

—— Tiergallen auf Flechten. Op. cit. lxvi, pp. 61–103, 40 figs. (1929, 3).

—— Pilz-, Tier- und Scheingallen auf Flechten. Tom. cit. pp. 459–514, 60 figs.

Bornmüller, Josef. Zur Flechtenflora Macedoniens. Magy. Bot. Lap. xxvii, pp. 98–104 (1929).

The lichens here enumerated were the results of a first collection in 1918 in the neighbourhood of Uskub. A list of 85 species determined by A. Zahlbruckner.

Bouly de Lesdain. Notes Lichénologiques. XXIII. Bull. Soc. Bot. France, lxxiv, pp. 436–9 (1927).

Notes on lichens from France and Italy, with descriptions of new species, varieties and forms. A new *Verrucaria* from Mexico is included.

Cajander, A. K. The Theory of Forest Types. Acta Forest. Fenn. xxix, 108 pp. (1926). See op. cit. lxxvi, Bibliogr. pp. 818–19 (1929). Papers not seen.

In dry forests lichens are abundant, especially *Cladina* spp. In wet forests mosses preponderate.

Cappelletti, Carlo. Studi su la vegetazione resinicola. Ann. di Botanica, xvi, pp. 253–96, 1 pl. (1924).

Among other resinous plants *Biatorella difformis* Wain. and *B. resinae* Mudd were examined as to their status as lichens or fungi. In each case the symbiotic association with gonidia was observed.

—— Nuove osservazioni sul ciclo biologico di *Biatorella difformis*. Op. cit. xvii, pp. 1–3 (1926).

Cappelletti has made further cultures from spores of this resinous plant. Growth was slow and there was a final degeneration of the hyphae. *Coniothyrium resinae* developed in the culture, its derivation was doubtful.

Cengia-Sambo, M. Licheni della Terra del Fuoco raccolti da G. B. de Gasperi nel 1913. Nuovo Giorn. Bot. Ital. xxxiii, pp. 84–91 (1926).

The lichen flora is subpolar owing to cold currents from the south. *Cladonia rangiferina* and *C. alpestris* grow in abundance, as in Arctic regions.

—— Licheni di Rodi. II. Op. cit. xxxiv, pp. 829–40 (1927).

The author publishes 41 lichens from various localities in Rhodes. The lichen flora resembles that of the Eastern Mediterranean.

—— Un Lichene epifillo su una Palma di Serra dell' Orto botanico di Firenze. Op. cit. xxxv, pp. 257–8 (1928).

The lichen though sterile was determined as a *Lecanora* sp. which grew normally on palm leaves in tropical lands.

—— Ecologia dei Licheni. Atti Soc. Ital. Sci. Nat. lxvii, pp. 264–83 (1928); and op. cit. lxviii, pp. 1–13 (1929).

Cengia-Sambo, M. Di un Lichene di Marmorica. Bull. dell' Orto Bot. Napoli, IX, pp. 17–23 (1928). See Bot. Centralbl. CLVII, p. 72 (1929). Paper not seen.

—— I Licheni come Indicatori del Clima. Nuovo Giorn. Bot. Ital. XXXVI, pp. 338–59 (1929).

—— "Lichenes" in Flora Somala (Emilio Chiovenda). Sindic. Ital. Roma, pp. 340–57 (1929).

Choisy, Maurice. Qu'est-ce que *Pseudo-leptogium* Müll.-Arg.? Arch. Bot. I, pp. 139–40 (1927).
A discussion of the species that have been included under *Pseudo-leptogium diffractum.*

—— Sur la Morphologie des Hyphes Ascogènes dans le genre *Lecidea* (Lichens). Bull. Soc. Mycol. France, XLIII, pp. 209–10, 2 figs. (1927).

—— Une nouvelle espèce de Lichen: *Toninia* (*Thalloedema*) *alluviicola* Choisy. Bull. Soc. Linn. Lyon, VI, n. 3, p. 21 (1927).
Associated previously with *T. vesicularis* but with a thinner cortex, K + violet, and spores constantly 1-septate.

—— Sur le phylétisme des Ascomycètes du genre *Cladonia* (Lichens). Bull. Soc. Mycol. France, XLIII, pp. 267–71 (1927).

—— Icones Lichenum Universalis. Fasc. I, 8 pls. Lyon (1928), 2°.

—— La phylogénie probable des Peltigéracées et du genre *Nephroma* Ach. Ann. Soc. Linn. LXXIV, 6 pp. (1928). See Bot. Centralbl. CLVII, p. 72 (1928). Paper not seen.

—— Sur un cas tératologique curieux du *Parmelia prolixa.* Arch. de Bot. II, pp. 82–4, 2 figs. (1928).
A *Parmelia* apothecium was invaded by a parasitic fungus; the thallus had totally disappeared owing to the attack.

—— Existe-t-il un nouveau Type de Spores en Mycologie? Bull. Soc. Roy. Bot. Belgique, LXI, pp. 71–4 (1928).

—— A propos d'une nouvelle espèce de Lichen, *Toninia* (s.g. *Thalloedema*) *aluviicola* Choisy. Bull. Soc. Bot. France, Sér. 5, IV, pp. 80–2 (1928).
The new species grows mostly on glacial clay.

—— Genres nouveaux pour la Lichénologie dans le groupe des Lécanoracées. Op. cit. Sér. 5, V, pp. 521–7 (1929).
A further exposition of the author's views on phylogeny and classification. Many new groupings are proposed.

—— La Morphologie du genre *Cladonia*, Lichen Discomycète. Bull. Soc. Mycol. France, XLV, pp. 184–8 (1929).

Crozals, A. de. Essai sur les Collémacées des Environs de Toulon. Ann. Soc. Hist. Nat. Toulon, pp. 16–73 (1927).
The list of Collemaceae has been increased in the Toulon district to 77 species, proving that they are on the whole plants of warmer regions.

Cypers-Landrecy, V. Beiträge zur Kryptogamenflora des Riesengebirges und seiner Vorlagen. Lotos, LXXIV, pp. 1–18 (1926).
A long list of the lichens collected in other than the Silesian side of the mountains. Localities and habitats are fully given.

Danilov, A. N. Introduction à la synthèse du lichen *Leptogium Issatschenkii* Elenk. Bull. Jard. Bot. Princ. U.R.S.S. XXVIII, pp. 225–64, 2 pls. 12 figs. (1929). Russian with French résumé.

—— Nostoc en état de symbiose. Arch. Russ. Protist. VI, pp. 83–92, 1 pl. (1927). Russian with French résumé. See Bot. Centralbl. CLVI, p. 359 (1929).

Darbishire, O. V. Ueber das Wachstum der Cephalodien von *Peltigera aphthosa.* Ber. Deutsch. Bot. Ges. XLV, pp. 221–8, 1 pl. (1927).

—— Roccellaceae Mass. (Nyl.). Die Pflanzenareale. Zweite Reihe, Heft 1, pp. 1–4, 5 pls. (1928).

DEECKE, W. Flechtenrasen in Löss. Zeitschr. Deutsch. Geol. Ges. Mon. Ber. LXXX, pp. 374–9, 2 figs. (1928). See Bot. Centralbl. CLVII, p. 232 (1929).
Minute soil channels, "tubes," occurred in the Löss district, considered by Deecke to be the remains of *Cladonia rangiferina*, dating from the glacial tundra period.

DEGEN, A. v., JUL. GÁYER und JOSEF SCHEFFER. Die Flora des detrekö-esütörtöker Moores und des östlichen Teiles des Marchfeldes. Magy. Bot. Lapok, XXII, pp. 1–116 (1923). (Lichenes, H. H. Suza, pp. 47–52.)

DODGE, CARROLL W. Lichens of the Gaspé Peninsula, Quebec. Rhodora, XXVIII, pp. 157–61, 205–7 and 225–32 (1926).
The Gaspé Peninsula is in Eastern Quebec. The list summarises the work of other collectors as well as that of the writer. The Cladoniaceae received the most attention; a large number of species were collected and determined.

—— A Synopsis of *Stereocaulon*, with notes on some exotic species. Ann. Crypt. Exot. II, 2, pp. 93–153 (1929).

DOMIN, KARIL. The Relations of the Tatra Mountain Vegetation to the Edaphic Factors of the Habitat. Acta Soc. Bohemica, VI–VII, pp. 133–64 (1928).

DU RIETZ, G. EINAR. Die Hauptzüge der Vegetation der Insel Jungfrun. Svensk Bot. Tidskr. XIX, pp. 323–46 (1925).

—— Om släktena *Evernia* Ach., *Letharia* Zahlbr., emend. D. R. och *Usnea* Ach. Op. cit. XX, pp. 89–93 (1926).

—— Skandinaviens *Stereocaulon*-Arter. Tom. cit. pp. 95–6.
A synoptic key to the species of *Stereocaulon* in Scandinavia, eleven in all.

—— Lichenologiska Fragment. VIII. Ett Bidrag till Åsele Lappmarks Lavflora. Tom. cit. pp. 281–3.
An account of lichens collected during a journey to Norrland, Åsele. The Cladoniae were the most abundant lichens.

—— *Gyrophora rigida* D. R. in North America. A new member of the West-Arctic Element in the Scandinavian Mountain-Flora. Op. cit. XXII, pp. 278–81 (1928).

—— Zur Kenntnis der Flechtenreichen Zwergstrauchheiden im Kontinentalen Südnorwegen. Svensk Vaxt. Sällsk. Handl. IV, pp. 1–80, 8 figs. (1925).

—— Zur Flechtenflora von Sudgeorgien. Nyt Mag. Naturvidensk. LXIV, pp. 229–33 (1926).
The most important records were subantarctic species, but the majority have also been recorded from Northern Europe.

—— The Lichens of the Swedish Kamtschatka Expeditions. Ark. för Botanik, XXII, N. 13, pp. 1–25, 2 pls. (1929).

DU RIETZ, GRETA SERNANDER. *Parmelia tiliacea* en Kustlav och Marin inlandsrelikt i Skandinavien. Svensk Bot. Tidskr. XX, pp. 352–65, 3 figs. (1926).
A paper on the distribution of the *Parmelia*.

EHRLICH, ERNST. Die Pflanzen des Bezirkes Friedland—Lichenes. Mitt. Ver. Naturfr. Reichenberg, XLIX, pp. 83–5 (1927). See Hedwigia, LXVII, Beiblatt, p. 146 (1927).

ELENKIN, A. A. Sur les principes de la classification des Lichenes. Journ. Soc. Bot. Russie, XI [1926], pp. 245–72 (1927). See Ann. Mycol. XXVII, p. 141 (1929). Paper not seen.

—— Sur les principes théoriques servant à détailler les rangs essentiels du système combinatif des lichens. Bull. Jard. Princ. U.R.S.S. XXVIII, pp. 302–5 (1929).

—— Sur certaines conséquences du principe combinatif dans le système des lichens. Tom. cit. pp. 442–5. French résumé.

ERICHSEN, C. F. E. Flechten bei Hoch. Röper. Neue Ergebnisse der Erforschung unserer Pflanzenwelt. Verhandl. Naturwiss. Ver. Hamburg, 4 Folge, II, pp. 174–7. See Hedwigia, LXVII, Beiblatt, p. 146 (1927).

Erichsen, C. F. E. Die Flechten des Schutzgebietes bei Süderlügum. Beitr. zur Naturdenkmalpflege, XII, pp. 303–7 (1928).

—— Die Renntierflechte und ihr Vorkommen in Schleswig-Holstein. Heimat, XXXIX, pp. 207–10 (1929). See Bot. Centralbl. CLVII, Heft 14, p. 104 (1929). Paper not seen.

Notes on the immense fields of reindeer lichens in Norway.

—— Die Flechten des Moränengebiets von Ostschleswig. Verh. Bot. Ver. Prov. Brandenb. LXX, pp. 128–72, 1 sketch-map (1928). Tom. cit. pp. 173–223. Op. cit. LXXI, pp. 85–129 (1929). Op. cit. LXXII, pp. 1–68, 5 pls. (1930).

Evans, Alexander W. Notes on Connecticut Lichens. Rhodora, XXIX, pp. 97–105 (1927).

Additional lichens to the list already published and notes on localities.

Evans, Alexander W. and Rose Meyrowitz. Catalogue of the Lichens of Connecticut. State Geol. Nat. Hist. Survey Bull. N. 37, pp. 1–48 (1926).

A list of lichens and of collections from 1855 onwards, with notes on the collectors and the localities.

Fink, Bruce. New Species of Lichens from Porto Rico. I. Graphidaceae. Mycologia, XIV, pp. 206–21 (1927).

Firbas, Franz. Vegetationsstudien auf dem Donnersberge im Böhmischen Mittelgebirge. Lotos, LXXVI, pp. 113–72, 4 pls. 6 figs. (1928).

In an account of the general vegetation lichens are recorded from oak and grass associations (p. 121) and from blocks of stone (p. 131).

Fokin, A. and P. N. Nikolski. The Lichen flora of Gouv. Wjatka. 1. Peltigeraceae. Arb. Staatl. Mus. Wjatka, 22 pp. (1927) (Russian). See Bot. Centralbl. CLV, p. 304 (1928).

Fóriss, F. Beiträge zur Kenntnis der Flechtenflora des Kudsirer Hochgebirges. Botan. Közl. XXV, pp. 59–91 (1928).

An account of 337 lichen species, 16 species and 43 varieties being new for Hungary. Distribution is influenced more by vertical than by horizontal distance. The region of leafy woods is richer in species than the high tablelands.

Fraymouth, Joan. The Moisture Relations of Terrestrial Algae. III. The Respiration of certain Lower Plants, including Terrestrial Algae, with Special Reference to the Influence of Drought. Ann. Bot. XLII, pp. 75–100, 6 figs. (1928).

Frey, Edouard. Bemerkungen über die Flechtenvegetation Skandinaviens, verglichen mit derjenigen der Alpen. Veröffentl. des Geobotan. Inst. Rübel in Zürich, Heft 4, pp. 210–59, 3 pls. 4 figs. Bern (1927). See Ber. Schweiz. Bot. Gesell. XXXVII, p. 111 (1928). Paper not seen.

—— Flechten. Ber. Schweiz. Bot. Gesell. XXXVI, pp. 48–58 (1927). Op. cit. XXXVII, pp. 110–24 (1928). Op. cit. XXXVIII, pp. 107–21 (1929).

In each paper is given an account of Swiss Lichenology: a Bibliography of publications bearing on the subject, and a list of species or varieties new to Switzerland, with descriptions and notes.

—— Drei neue Flechtengattungen. Tom. cit. pp. 43–61, 7 figs.

—— Beiträge zur Biologie, Morphologie und Systematik der Umbilicariaceen. Hedwigia, LXIX, pp. 219–52, 9 figs. (1929).

—— Zwei lichenologische Entdeckungen. Mitt. Nat. Ges. Sonderdr. 5, I, II, 2 pp. Bern (1929).

A new genus and species of Ephebaceae, *Lecanephebe Meylani*, with lecanorine apothecia.

Frey, E. et Ochsner, F. Contribution à la connaissance de la végétation lichénique et muscinale. Rev. d'Auvergne, Arvernia, XVI, pp. 50–84 (1926). See also, Hedwigia, LXVII, Beiblatt, p. 146 (1927).

FRY, E. JENNIE. The Mechanical Action of Crustaceous Lichens on Substrata of Shale, Schist, Gneiss, Limestone and Obsidian. Ann. Bot. XLI, pp. 437–60, 2 pls. 22 figs. (1927).

—— The Penetration of Lichen Gonidia by the Fungal Constituent. Op. cit. XLII, pp. 141–8, 6 figs. (1928).

GALLOE, O. A Natural History of the Danish Lichens. Original Investigations based upon new Principles. Copenhagen (1927). Part I, pp. 1–93, 16 pls.
A first part of a large work dealing with lichenology in general. No second part has yet been issued.

GARSIDE, S. The Structure and Mode of Reproduction of *Siphula tabularis* Nyl. Trans. Brit. Mycol. Soc. XIV, pp. 60–9, 1 pl. 4 figs. (1929).

GILLET, A. Quelques Lichens corticoles de Poligny (S.-et-M.). Bull. Ass. Nat. Vallée du Loing, X, p. 90 (1927). Paper not seen.

—— Lichens des Grottes de Recloses (S.-et-M.). Op. cit. XI, p. 151 (1928). See Bull. Soc. Bot. France, LXXVI, Biblio. p. 911 (1929). Paper not seen.
In the Recloses caverns there are few species of lichens, chiefly growths of *Lepraria*.

GILTAY, L. Notes Lichénologiques. Bull. Soc. Bot. Belgique, LXI, pp. 120–2 (1929).
Notes on the occurrence of *Cetraria islandica* in Belgium—usually on siliceous soil on heather moorland.

GOEBEL, K. Morphologische und biologische Studien. VII. Ein Beitrag zur Biologie der Flechten. Ann. Jard. Bot. Buitenzorg, XXXVI, pp. 1–83, 2 pls. (1926).

—— Die Wasseraufnahme der Flechten. Ber. Deutsch. Bot. Ges. XLIV, pp. 158–61 (1926, 2).

—— Morphologische und biologische Bemerkungen. Induzierte Dorsiventralität bei Flechten. Flora, CXXI, pp. 177–88, 3 figs. (1926, 3).

GRAY, FRED W. An Explanation of the Occurrence of Certain New Cladonias. Bryologist, XXX, pp. 23–5 (1927).
The stages in lichen succession are considered and reasons for appearance and disappearance of Cladoniae suggested.

GYELNIK, W. Ueber eine neue Flechte nebst kritischen Bemerkungen ueber *Peltigera aphthosa* (L.) Willd. Magy. Bot. Lapok (Ungar. Bot. Blätter), XXIV, 1925, pp. 79–80 (1926). See Hedwigia, LXVII, Beibl. p. 64 (1927).

—— Nédány *Peltigera*-adat Japánból.—Einige *Peltigera*-Daten aus Japan. (Hungarian and German.) Magy. Bot. Lapok, XXV, pp. 252–4 [1926] (1927).
A small collection made by Abbé Faurie now in the Vienna Herbarium; two new species were determined.

—— Lichenologiai Közlemények 1–3. Op. cit. XXVI, pp. 46–7 [1927] (1928).
Notes on lichens from China, Constantinople and Brazil.

—— Lichenologiai Közlemények 4–7. Op. cit. XXVII, pp. 91–3 (1929). (Hungarian and English.)
An account of three species of *Peltigera* from tropical Africa.

—— Lichenologische Mitteilungen 8–19. Tom. cit. pp. 57–65. (Hungarian and German.)
A series of notes on various lichens. He finds that *Parmelia rosaeformis* Ach. is a first name for *P. sulcata* Tayl. and that *P. Bornmülleri* Zahlbr. is *P. glabra* Tayl.

—— Les formes du *Parmelia verruculifera* Nyl. Tom. cit. pp. 173–5, 1 fig. (Hungarian and French.)

—— *Peltigera*-tanulmányok. Bot. Kozlem. XXIV, pp. 122–40, 4 figs. (1927). *Peltigera* studies. Résumé in German.

—— Beiträge zur Flechtenvegetation Ungarns. I. Com. Szabolcs. Folia Crypt. Zeitschr. Erf. Ungar. Kryptogamen Flora, I, pp. 237–42 (1926) (Hungarian); and II. Op. cit. pp. 577–604 (1928).

GYELNIK, W. (Budapest). *Peltigera*-Daten. Hedwigia, LXVIII, pp. 1–4 (1928).
A list of *Peltigera* species in the Berlin Museum, from various regions, determined by Gyelnik. He describes new species from China, Mexico and Columbia, with a new form of *P. rufescens* from Teneriffe.

—— Peltigerae novae et criticae. Österr. Bot. Zeitschr. LXXVII, pp. 220–6 (1928).
The author contributes four new species and several varieties to the genus from N. Zealand, S. America, N. America and Austria.

HANSEN, H. MØLHOLM. Hammer Bakkev. En Botanisk Undersøgelse ivaerksat of Dansk Botanik Forening. V. Likenen- og Mosvegetationen. Bot. Tidskr. Københ. XXXIX, pp. 279–88 (1926).
An ecological account of the district explored. A list of the lichens is given.

HANSEN, H. MØLHOLM and MOGENS LUND. Die Danske Arter af Slaegten *Cladonia*. Bot. Tidsk. XLI, pp. 1–80, 4 pls. (1929).

HARMAND, A. Lichens d'Indo-Chine recueillis par M. V. Demange. Ann. Crypt. Exot. I, pp. 319–37 (1928).
Lichens from Annam and Yunnan-Fau (China) and also from Singapore Botanic Garden. 82 species, 12 varieties and 14 forms are listed, a considerable number new to science.

HARSHBERGER, J. W. Tundra Vegetation of Central Alaska. Directly under the Arctic Circle. Proc. Amer. Phil. Soc. LXVII, pp. 215–34, 16 figs. (Lichen Societies, pp. 226–7 with fig. 12) (1928).

HARTLEY, J. W. and J. A. WHELDON. Lichens of the Isle of Man. North Western Naturalist (Supplement), II, pp. 13–38 (1927).
The final instalment of lichens from the Isle of Man.

HÄYRÉN, E. *Siphula* ceratites from Petsamio. Memoranda Soc. pro Faun. et Flor. Fenn. IV, pp. 48–9 (1928).

HILITZER, ALFRED. Réception et évaporation de l'eau chez le thalle des lichens. Bull. Intern. Acad. Sci. Bohème, pp. 1–19, 6 pls. (1927).

—— Notes sur quelques Lichens récoltés dans les Jeseniky. Preslia, V, 3 pp. (1927).
A preliminary floristic account of lichens of the Jeseniky Mountains. A northern species *Parmelia infumata* he judged to be a relic of glacial times.

—— Příspěvky k Lišejníkůni Šumavy a Pošumavi. (Les lichens des lydites des environs de Klatovy. French résumé.) Zol. otisk z Časopisu Národního Musea, pp. 1–15 (1927).
Study of lichens on lydite rocks—15 associations were recognised. Lydite lichens he found were very different from those on schists.

HILLMAN, JOH. Übersicht über die in der Provinz Brandenburg bisher beobachteten Flechten. Verh. Bot. Ver. Prov. Brandenb. LXVIII, pp. 189–201 (1926); op. cit. LXX, pp. 44–54 (1928).
A description of Brandenburg lichens with considerable critical work.

—— Studien über die Flechtengattung *Teloschistes* Norm. Hedwigia, LXIX, pp. 303–43, 2 figs. (1930).

HOEG, O. A. Lichenological Notes. 1–2. Kgl. Norske Vidensk. Selsk. Handl. I. N. 60, pp. 179–81, 1 fig. (1929). See Centralbl. CLVI, p. 71 (1929). Paper not seen.

HOLLERBACH, M. M. Einige Nachträge zur Anatomie der Wasserflechte *Collema* (?) *Ramenskii* Elenk. Bull. Jard. Bot. Princ. U.S.S.R. XXVII, pp. 306–13, 1 pl. (1928). Russian with German résumé.

HOWLAND, LUCY J. The Moisture Relations of Terrestrial Algae. IV. Periodic Observations of *Trentepohlia aurea* Mart. Ann. Bot. XLIII, pp. 173–202, 15 figs. (1929).

HRUBY, JOHANN. Die Pflanzengeographische Gliederung Mährens und Schlesiens. Verhandl. Naturf. Ver. Brünn, LIX [1922–4], pp. 69–88 (1925). See Hedwigia, LXVII, Beiblatt, p. 148 (1927).

HURST, CECIL, P. East Wiltshire Lichens. Wiltshire Arch. and Nat. Hist. Mag. XLII, pp. 1–10 (1923).

A list of eighty-one lichens collected in Savernake Forest and near Great Bedwyn.

JAAG, OTTO. Nouvelles recherches sur les gonidies des Lichens. Compt. Rend. Soc. Phys. Hist. Nat. Genève, XLV, pp. 28–32 (1928).

—— Sur les gonidies des Parmelias et leur spécificité. Acta Soc. Helvet. Sci. Nat. CIX, pp. 192–3 (1928, 2).

—— Recherches expérimentales sur les gonidies des lichens appartenant aux genres *Parmelia* et *Cladonia*. Bull. Soc. Bot. Genève, XXI, pp. 1–119, 6 pls. 5 figs. (1929).

JEANJEAN, A.-F. Lichens observés dans le Lot-et-Garonne. Actes Soc. Linn. Bord. LXXVII, pp. 195–281 (1925).

The species 339 in number were mainly determined by Dr Bouly de Lesdain.

KEISSLER, KARL. Ueber die als Pilze anzusehenden Arten unter den Norman'schen Moriolaceen. Nyt. Mag. Naturv. B. LXVI, pp. 77–92 (1927).

Keissler has concluded from his study of the family that the genera and species are mostly fungi.

—— Systematische Untersuchungen über Flechtenparasiten und lichenoide Pilze. Ann. Naturhist. Mus. Wien, XLI, pp. 157–70, 2 figs. (1927).

—— Flechtenparasiten. Rep. Sci. Results Norw. Exped. to Novaya Zemlya, 1921. No. 38, pp. 1–5, Oslo (1928).

Twelve species of lichen parasites were observed. They occurred chiefly on crustaceous lichens.

—— Systematische Untersuchungen über Flechtenparasiten und lichenoide Pilze. Ann. Naturhist. Mus. Wien, XL, pp. 99–106 (1928).

—— Die Flechtenparasiten Deutschlands, Oesterreichs und der Schweiz mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. Rabenhorsts Krypt. Fl. von Deutschl., Oesterr. und der Schweiz. VIII, Lief. 1, pp. 1–240, 149 figs. (1930).

KNEUCKER, A. Eine neue Flechte vom Sinai und vom Ufer des Toten Meeres. Allg. Bot. Zeitschr. XXV, p. 43 (1926).

The lichen *Psorotichia sinaiensis* was determined by Vainio. It has a thin yellowish thallus.

KNIEP, HANS. Die Sexualität der niederen Pflanzen. Jena, Gustav Fischer (1928), 544 pp. Anhang: 1, Lichenes, pp. 385–8, 1 fig.

Kniep in this short discussion accepts the sexual character of the pycnidia as spermogonia, and also the function of the "trichogyne" in fertilisation.

KNIGHT, H. H. Lichens of the Marlborough Foray and Lichens of Aviemore District. Trans. Brit. Mycol. Soc. XIII, pp. 149–50 and 314–16 (1928).

Lichens from two widely separated localities. In the south they were mainly corticolous, in the north (Inverness-shire) mainly saxicolous, with many northern and alpine forms.

KNOWLES, M. C. The Lichens of Ireland. Proc. Roy. Irish Acad. XXXVIII, Sect. B, No. 12, pp. 179–434 (1929).

KOLLHOFF, W. Verzeichnis der auf der grenzmärkischen Studienfahrt 1927 beobachteten Flechten nebst einigen Moosen. Abh. und Ber. Naturw. Abt. grenzmärk. Ges. z. Erforsch. u. Pflege der Heimat. Schneidemühl, II, pp. 45–57 (1927). See Ann. Mycol. XXVII, p. 142 (1929). Paper not seen.

—— Die Flechten Schneidemühls. Tom. cit. pp. 62–8. Paper not seen.

KOPPE, F. Verzeichnis einiger in der Grenzmark Posen-Westpr. gesammelter Flechten. Tom. cit. pp. 58–61. Paper not seen.

KROHN, V. Das Wesen der Flechten durch Serum-Reaktionen beleuchtet. (Vorl. Mitt.) Helsinski [Sana-A.-G.], pp. 1–10, 13 pls. (1927). See Hedwigia, LXVII, Beiblatt, p. 146 (1927). Paper not seen.

Kušan, Frau. Predradnje za floru lišajeva Hrvalske. I. Izvještaj. Acta Bot. Inst. Bot. Univ. Zagrebensis, III, pp. 1–40 (1928). Croatian with German résumé. (Vorarbeitung zu einer Flechtenflora Kroatiens. I. Mitteilung.)

The writer, finding that little was known about the lichens of Croatia, has collected over the territory, and has compiled a list of 163 species. One, new to science, *Biatorella biformis*, is characterised by large apothecia.

Kutak, V. Příspěvek k lichenologii Krkonoš. (Notes sur les lichens des Krkonos.) Preslia, IV, pp. 20–9 (1926).

—— Tretí příspěvek ku kvetene ěéskych lisejníků. 3. Contribution à la connaissance des lichens de la Bohème. Op. cit. V, pp. 36–51 (1927). See Bull. Soc. Bot. France, LXXVI, p. 178 (1929). Paper not seen.

Lange, H. Zur Flechtenflora des Erzgebirges (Das obere Zschopaugebiet). Hedwigia, LXIX, pp. 56–83 (1929).

Light, S. Stuart. The Fauna and Flora of Apple Bark. Ann. and Mag. Nat. Hist. Ser. 9, XVII, pp. 126–49 (1926).

Lynge, Bernt. Peltigeraceae in the Copenhagen Arctic Herbarium. Dansk. Bot. Ark. V, N. 11, pp. 1–13 (1928).

—— Lichens from Novaya Zemlya (excl. of *Acarospora* and *Lecanora*). Report of the Scientific Results of the Norwegian Expedition to Novaya Zemlya 1921, N. 43. Det Norske Vidensk. Akad. Oslo, pp. 1–298, 3 pls. and map (1928).

—— Lichens from the Taimir Peninsula. Norwegian North Polar Exp. with the "Maud" 1918–25. Scientific Results. Geofysisk Inst. Bergen, V, N. 1, pp. 11–15 (1929).

Magnusson, A. H. New Species of Lichens in the North of U.S.S.R. Bull. Jard. Bot. Princ. U.S.S.R. Leningrad, XXVI, pp. 1–12 (1927).

The lichens are from Lappland, Finnland, Nova Zembla, Isle of Kolguev and the Arctic Ural. Four species are new to science.

—— Descriptions of New or not Properly Defined Lichens. Medd. Från Göteborg's Bot. Tradgard, III, pp. 11–23 (1927).

Descriptions of new species from North Russia and from N. and S. America.

—— New or Interesting Swedish Lichens. IV. Bot. Not. (1927), pp. 115–27.

—— New Species of Lichens in the North of U.S.S.R. Bull. Jard. Bot. Princ. U.S.S.R. XXVI, pp. 365–70 (1928).

—— *Acarospora*. Report of the Scientific Results of the Norwegian Expedition to Novaya Zemlya, 1921, N. 34. Det Norske Vidensk. Akad. Oslo, pp. 1–7 (1928).

—— Flora över Skandinaviens Busk- och Bladlavar utarbetad huvudsakligen för Nybörjare. Stockholm, Norstedt and Söner, pp. 1–127, 6 pls. 11 figs. (1929).

—— New or Interesting Swedish Lichens. V. Bot. Not. (1929), pp. 110–22.

—— A Monograph of the Genus *Acarospora*. K. Svenska Vetensk. Handl. VII, pp. 1–400, 18 maps (1929).

—— The Yellow Species of *Acarospora* in North America. Mycologia, XXI, pp. 249–60 (1929).

Many of the species have not previously been recorded for America. Descriptions are given of eight species new to science.

Maheu, J. Contribution à la Lichénographie du Rif (Maroc). Cavanillesia, Barcelona, I, pp. 53–9 (1928). See Bot. Centralbl. CLV, p. 100 (1928).

Maheu, Jacques et Abel Gillet. Lichens de l'Ouest de la Corse. Hist. Nat. Autun, XXVII, pp. 49–111 (1914).

The authors have recorded in the above paper 197 species, with localities and many instructive notes. One species, *Lecanora* (*Squamaria*) *erminea* Auc., is a new species. They give a list, so far as was then known, of the various species and varieties, with index.

Maheu, Jacques et Abel Gillet. Contribution à l'étude des Lichens des Iles Baléares. Bull. Soc. Bot. France, LXVIII, pp. 426–36; 516–25 (1921). Op. cit. LXIX, pp. 41–50; 96–104; 196–201 (1922).

The authors collected the lichens on several visits to the Islands. They have recorded in all 216 species, varieties or forms, a few being new to science. An account is given of the geological structure of Majorca and Minorca.

—— —— Deuxième Contribution à l'étude des Lichens du Maroc. Op. cit. LXXII, pp. 858–70 (1925).

We are told by the authors that the "first contribution" was published in the Compte-rendu de la Session du Maroc (1921). The species enumerated now were collected by Madame Gillet at Boulhaut near to Casablanca and at Tangiers. Several new species are described.

—— —— Lichens de l'Est de la Corse. Berthier, Dijon, 114 pp. 3 pls. (1926).

The paper includes a foreword by P. Genty of the Botanic Gardens, Dijon, describing how the lichens collected by Zschacke of Bernburg came into possession of the Botanic Gardens. The writers enumerate 300 species. Five species and six varieties are new to science.

Malme, Gust. O. A. N. Nagra Lavar från Trosatrakten. Svensk Bot. Tidskr. XX, pp. 52–9 (1926).

A varied series of lichens are recorded with habitats and notes.

—— Die in Regnellschen Herbar aufgewahrten Arten der Flechtengattung *Lecanactis* (Esch.) Wainio. Ark. för Bot. XX, N. 2, pp. 1–6 (1926).

Only four species are recorded by Malme: the most abundant *Lecanactis insignior* var. *fusca* grew on the bark of trees.

—— Lichenologiska Notiser. Svensk Bot. Tidskr. XXI, pp. 251–9 (1927) (Swedish).

Notes on northern species of *Rinodina* and *Buellia*.

—— Ytterligas några lavar från Trosatrakten. Tom. cit. pp. 361–4, 1 fig.

Further lichens from the neighbourhood of Trosa.

—— Buelliae itineris Regnelliani primi. Ark. för Bot. XXI, N. 14, pp. 1–42, 5 figs. (1928).

—— Lichenes pyrenocarpi aliquot in Herbario Regnelliano asservati. Ark. för Bot. XXII, N. 6, pp. 1–11 (1929).

—— Pyrenulae et Anthracothecia Herbarii Regnelliani. Tom. cit. N. 11, pp. 1–40, 3 figs. (1929).

Mameli-Calvino, E. e A. Agostini. Secondo contributo alla Lichenologia del Forlivese. Nuovo Giorn. Bot. Ital. XXXV, pp. 525–35 (1929).

Martin-Sans, E. Un herbier du Frère Saltel. Mousses et Lichens de la collection Herrmann. Bull. Soc. Hist. Nat. Toulouse, LVI, pp. 116–46 (1927). See Bot. Centralbl. CLV, p. 426 (1928).

A collection of lichens, 148 species, from the French Department Aveyron. The French lichenologist Saltel explored the region for lichens in 1898–1904.

Mattick, Fritz. Die Flechten des Naturschutzparkes in den Hohen Tauern. Hedwigia, LXIX, pp. 262–86 (1929).

Menzies, James. Lichens: With Notes on Local Species. Trans. Perthshire Soc. Nat. Sci. VIII, pp. 159–73 (1926–7).

Presidential address giving a general account of lichens in Perthshire.

Mereschkovsky, C. de. Matériaux pour une monographie du genre *Graphis*. Candollea, I, pp. 473–9 (1922–4).

An account of *Graphis scripta* with many varieties.

—— Notes critiques sur quelques espèces de la Crimée. Tom. cit. pp. 491–9.

The author discusses various species wrongly recorded for the Crimea.

Merrill, G. K. A List of the Peruvian Lichens by G. Bues. Bryologist, XXX, pp. 83–8 (1927). Also in Rev. Univ. Cuzco-Peru, XIII, pp. 171–9 (1929).

The lichens—mostly of the larger species—were collected in 1919 and 1920, and are now in Yale University.

MERRILL, G. K. A New List of Alaskan Lichens in the Genus *Cladonia*. Bryologist, XXXII, pp. 41–50 (1929).

MESSIKOMMER, EDWIN. Biologische Studien im Torfmoor von Robenhausen unter besonderer Berücksichtigung der Algenvegetation. Inaug. Diss. Mitt. aus dem Bot. Mus. Univers. Zürich, CXXII, Lichens, pp. 113–15 (1927). See Ber. Schweizer. Bot. Gesell. XXXVII, p. 111 (1928). Paper not seen.

A list of the lichens found on bog moors.

MÉTHÉRY, G. Étude anatomique et microchimique et essai de Classification des Parméliacées. Bull. Soc. Hist. Nat. Auvergne (1928), N. 13, pp. 18–33. See Bot. Centralbl. CLVI, p. 71 (1929). Paper not seen.

MIGULA, WALTER. Flora von Deutschland, Oesterreich und der Schweiz. Abt. II. Kryptogamen-Flora. Die Flechten, IV, II. Lief., 42, 1929.

MIKHAILOVSKY, V. S. Lichenological Observations in the Kharkov District. (Russian with French résumé.) Ann. Sci. Chaire Bot. Charkov, I, pp. 89–112 (1927).

MOREAU, F. Les Lichens. Morphologie, Biologie, Systématique, Encyclopédie biologique. Paris, II, pp. 144, 65 figs. 2 pls. (1928).

MOREAU, M. et MME FERNAND. Les accidents homosymbiotiques de la surface des Lichens. Bull. Soc. Bot. France, Sér. 5, II, pp. 356–76, 15 figs. (1926).

—— Observations sur l'écologie et la sociologie des Lichens corticoles. Tom. cit. pp. 899–909.

—— Reproduction sexuelle chez les Lichens du genre *Collema* et la Théorie de Stahl. Comptes Rendus Acad. Sci. CLXXXII, pp. 802–4 (1926).

—— La signification du podétion des *Cladonia*. Bull. Soc. Mycol. France, XLII, pp. 249–54 (1927).

—— Les phénomènes cytologiques de la reproduction chez les champignons des Lichens. Le Botaniste, XX, pp. 1–66, 35 figs. (1928).

—— A propos de la signification du podétion des *Cladonia*. Réponse à M. Choisy. Bull. Soc. Mycol. France, XLIV, pp. 206–7 (1928).

The writers insist on their view that the podetium is purely thalline in origin and function.

MOTYKA, J. Materjaty do flory porostów Tatr. (Material for a Lichenflora of the Tatra.) Spraw. Kom. fizjogr. Polskie Akad. Umiej, LXI, pp. 1–16 (1927) (Polish). See Bot. Centralbl. CLV, p. 72 (1928).

—— Études sur les associations des Lichens établies sur les troncs des arbres aux environs de Grybou. Sylwana, XLV, pp. 1–35 (1927) (Polish with French résumé). See Bot. Centralbl. CLV, p. 72 (1928).

—— Guide Lichénologique de l'excursion dans les Tatras. Kraków (1928), 8 pp. 2 text-photo. See Bot. Centralbl. CLVII, p. 436 (1929).

Lists of the plants found give an idea of the richness of the lichen-flora.

NIENBURG, W. Anatomie der Flechten. Linsbauer: Handbuch der Pflanzenanatomie, II, Bog. 1–9, 137 pp. 183 figs. (1926). See Ber. Schweiz. Bot. Gesell. XXXVI, p. 49 (1927).

NIKOLOFF, A. P. Beitrag zur Flechtenflora Bulgariens. Bull. Soc. Bot. Bulgarie, II, pp. 25–8 (1928).

The author records a number of lichens of which 16 species are new to the Bulgarian Flora. They were collected from Pirin Rila and Stara Planina.

NIKOLSKY, P. N. Lichen Formations in the Pine Forest of Medvedok. (Russian with English summary.) Bull. Jard. Bot. Princ. U.R.S.S. XXVII, pp. 605–18 (1928).

—— Uebersicht den Literatur über die Flechten von Viatka Land, etc. Op. cit. XXVIII, pp. 608–23 (1929).

Russian with German note on the literature bearing on the lichens of the region and a list of the lichens recorded.

Nilsson, G. *Cetraria norvegica* (Lynge) DR. in Fennoskandia. Eine Übersicht anlässlich der Auffindung der Art in Schweden. Svensk Bot. Tidskr. xxii, pp. 515–27 (1928).

Nilsson supports Du Rietz in the view that *Cetraria lacunosa* is of American distribution, and a tree plant. *C. Norvegica* is isidiose and grows on rocks.

—— Lichenologiska bidrag. I. En lichenologisk exkursion till Halleberg. Bot. Not. (1929), 2, pp. 99–109.

Description of territory and a list of species collected.

—— Lichenologiska bidrag. II. Tom. cit. pp. 246–62, 2 figs.

Notes on a series of Swedish lichens—*Parmelia incolorata, Evernia divaricata* and others.

Ochsner, F. Studien über die Epiphyten-Vegetation der Schweiz. Jahrb. St Gall. Naturw. Gesell. lxiii, [1927], pp. 1–108, 15 figs. (1928).

Oxner, A. N. Zur Kenntnis der Flechtenflora an Austretungen festen Gesteins in der Ukraine. Bull. Jard. Bot. Kieff, v–vi, pp. 23–82, 1 fig. (1927) (Russian with German résumé); and pp. 823–4.

The papers deal with rock lichens and are largely ecological.

—— Neue Flechtenarten für die Ukraine. Tom. cit. pp. 89–92. Russian with German résumé.

A descriptive list of 10 species in the Ukraine.

—— Neue für die Ukraine Flechtenarten. Op. cit. vii–viii, pp. 71–3 (1928). Russian with German summary.

A list of 10 species new to the Ukraine.

—— Etwas für die Flechtenflora des Tschuktschenhalbinsel. Op. cit. ix, pp. 87–91, 1 fig. (1929). Russian with German summary.

A list of 17 species from the tundra of the North-Eastern Peninsula.

—— Neue Arten von *Aspicilia* aus Zentral-Asien. Op. cit. x, pp. 87–8 (1929).

Two new species of *Aspicilia* are described.

—— Neue für U.D.S.S.R. und seltene Flechtenarten. Ukrainian Botanical Review, iv, pp. 51–6 (1928). Russian with German summary.

The lichens recorded are new or rare forms: full biological notes are given.

—— Zehn für die Ukraine neue Flechtenarten. Bull. Jard. Bot. Kieff, ix, pp. 48–52 (1929). Russian with German summary.

The most interesting were *Physcia dimidiata* and *Gyrophora grisea*, both new to Russia.

—— Zur Systematik der Gattung *Lecania*. Tom. cit. pp. 62–3. Russian with German summary.

A new species of *Lecania* from Central Asia is described and *Lecidea expallescens* Nyl. is transferred to the genus.

—— Ueber *Ramalina Rjabuschinskii* Sav. Tom. cit. pp. 82–6. 4 figs. German and Russian.

Oxner found this species in the Far East near to Vladivostock. He decides that it is a true species and not a synonym of *R. Almquisti* Vain. as had been stated by Du Rietz.

Oye, Paul van. Écologie des Épiphytes des Troncs d'Arbres au Congo Belge. Rev. Gén. Bot. xxxvi, pp. 481–98, 1 fig. (1924).

Notes on the occurrence of lichens along with other epiphytes. Conditions are compared with those of Java discussed in a previous paper. (Tom. cit. pp. 12–30.)

Pakhunowa, W. G. A Note concerning the Epiphytal Lichens of Suhum and its outskirts. Moniteur Jard. Bot. Tiflis, 1926–7, pp. 57–60 (1927).

—— Lichens from the Mil-steppe (Azerbajdjan). Tom. cit. pp. 203–7. (See Ann. Mycol. xxvi, p. 468 (1927).) Paper not seen.

In the first paper the author records lichens that generally grow also on bark. *Biatorina Bouteillei* and *Pilocarpon leucoblepharum* alone seem to be obligate epiphytes. In the second paper she adds to our knowledge of soil formers, including therein *Collema granulatum, C. cristatum* and a form of *Squamaria muralis*.

PAUL, H. und VON SCHOENAU, K. Die naturwissenschaftliche Durchforschung des Naturschutzgebietes Berchtesgaden, III. Lichenes. Jahrb. Ver. zum Schutze der Alpenpl. I, pp. 69–71 (1929). See Hedwigia, LXIX, Beibl. p. 141 (1930).

PAULSON, R. Lichens of the Hereford Foray. Trans. Brit. Mycol. Soc. XII, pp. 87–90 (1927).
One new species, *Bilimbia sublubens*, and *Leptogium cataclystum* new to Britain are described.

—— Lichens of Spitsbergen and North-East Land. Journ. Bot. LXVI, pp. 77–81 (1928).

—— Lichens of Spitsbergen and North-East Land. Tom. cit. pp. 247–53.
Lichens collected by the Oxford University Arctic Expedition—119 species, 4 varieties. Notes are given on the influence of Arctic conditions.

—— Lichens from Yunnan. Tom. cit. pp. 313–19, 1 pl. and map.

PHILIPPS, JOHN F. V. The Influence of *Usnea* sp. (near *barbata* Fr.) upon the supporting tree. Trans. R. Soc. S. Africa, XVII, pp. 101–7 (1929).

PITMAN, EVADEL M. Journeying with Lichens and Hepatics in Maine. Bryologist, XXXII, pp. 110–11 (1929).
Notes of species observed during a stay in Maine.

PLITT, C. H. Succession in Lichens. Bryologist, XXX, pp. 1–4 (1927).

—— George K. Merrill. Op. cit. XXXI, pp. 65–71, with photogr. (1928).

—— Lichens occurring upon "Officinal" Drugs. Proc. Intern. Congress Plant Sci. 2, pp. 1382–1384 (1929).

PODPĚRA, JOSEF. Die Vegetationsverhältnisse der Pollauer Berge. Ein Beitrag zur Pflanzengeographie Mährens. Acta Bot. Bohemica, VI–VII, pp. 77–132, 4 pls. (1928).

PORTER, L. Rate of Growth of Lichens. Trans. Brit. Mycol. Soc. XII, pp. 149–52 (1927).

PORTER, C. L. and M. L. WOOLLETT. The Relation of *Cladonia* Mats to Soil Moisture. Torreya, XXIX, pp. 69–71 (1929).

RÄSÄNEN, VELI. Lichenes novi vel rariores e taeniis Ladogensibus. Meddel. Soc. Faun. and Flora Fenn. L, pp. 39–40 (1925).
A new species, *Aspicilia simoënsis*, and *Cetraria cucullata* var. *Vainioi* var. nov.

—— De *Usnea* nova in Sibiria inventa Animadvers. Syst. ex Herb. Univ. Tomskensis, N. 3, p. 1 (1927). See Hedwigia, LXIX, Beibl. p. 141 (1930).

RAUP, LUCY G. A List of the Lichens of the Athabasca Lake Region of North-Western Canada. Bryologist, XXXI, pp. 83–5; 100–4 (1928).
A large collection; 77 different species were determined mostly of northern distribution.

RICHARDS, P. W. Notes on the Ecology of the Bryophytes and Lichens at Blakeney Point, Norfolk. Journ. Ecol. XVII, pp. 128–40 (1929).

ROBBINS, C. A. *Cladonia Mateocyatha*, a new Species, and some variations in *C. Beaumontii*. Rhodora, XXVII, pp. 49–51 (1925).

—— Identity of *Cladonia Beaumontii*. Op. cit. XXIX, pp. 133–8, 1 pl. (1927).
A taxonomic discussion of the above *Cladonia* and of allied species.

—— The Identity of *Cladonia lepidota* Fr. Op. cit. XXXI, pp. 101–6, 1 pl. (1929).
This *Cladonia* species is distinct from *Cl. lepidota* Nyl. It belongs to the section with yellowish apothecia. Robbins adopts *C. piedmontensis* Merrill "as the first unpreoccupied specific name."

RUDOLPH, KARL, FRANZ FIRBAS und HANS SIGMOND. Das Koppenplanmoor im Riesengebirge. Lotos, LXXVI, pp. 173–222, 2 pls. (1928).
An ecological account of the region including a few lichens which were determined by J. Anders.

Sambo, E. I Licheni del Monte Ferrato (Toscana). Nuovo Giorn. Bot. Ital. xxxiv, pp. 333–38 (1927).
This region in Tuscany is composed of serpentine and granite, the trees mostly of pine.

Sampaio, G. y Luis Crespi. Liquenes de la Provincia de Pontevedra. Bol. Real Soc. Esp. Hist. Nat. xxvii, pp. 136–51 (1927).
A long and varied list of 218 species with habitat and locality.

Sántha, L. Zwei neue Physcien. Bot. Közlem. xxiii, pp. 128–32, 1 pl. (1926). (Hungarian.) See Ann. Mycol. xxvi, p. 162 (1928).

—— A. magyarországi *Physcia* félék monografiája, tekintettel az európai fajokra. Folia Crypt. Szeged (Hungary), 1, pp. 448–576, 10 pls. (1928). (Hungarian.)
Sántha records and describes species of *Physcia* in Hungary. The collection dates from 1753–1922.

Sbarbarro, Camillo. Licheni italiani nuovi o interessanti. Arch. Bot. Sist. Fitog. Genet. vi, pp. 9–15 (1930).
Species collected for Sbarbarro in Liguria, mostly determined by Bouly de Lesdain.

Schade, A. Ueber den Wärmegenuss einiger Moose und Flechten am Vallenberge. Sitzungsb. u. Abhandl. Naturw. Ges. "Isis," Dresden, pp. 38–55, 1927 and 1928 (1929). See also Hedwigia, lxix, Beibl. p. 144 (1930). Paper not seen.

Schaechtelin, J. et R.-G. Werner. Développement et Biologie de l'*Abrothallus parmeliarum* Sommef. Bull. Soc. Mycol. France, xlii, pp. 233–43, 1 pl. (1927).

—— —— Un Cas foudroyant de Parasymbiose. Le *Homostegia Piggotii* (Berk. and Br.) Karst, son développement biologique et physiologique. Bull. Soc. Mycol. France, xliv, pp. 232–40, 1 pl. (1928).

Schilling, Fr. Entwicklungsgeschichtliche und systematische Untersuchungen epiphyller Flechten. Hedwigia, lxvii, pp. 269–300, 2 pls. (1927).

Schmid, Günther. Endolitische Kalkflechten und Schneckenfrass. Biol. Zentralbl. xlix, pp. 28–35 (1929).

Schröder, Brno. Zellpflanzen Ostafrikas. Hedwigia, lxvii, pp. 141–9 (1927).
Large collections mostly from S. Africa have been determined by A Zahlbruckner in papers already noted (Ann. Mycol. xix, pp. 224–42 (1921) and Engl. Bot. Jahrb. lx, pp. 468–552 (1926)). In this paper Schröder lists the species that were collected by him in 1910, in all 73 species.

Servít, M. Dvě československé lokality lišegniku *Belonia russula* Krb. Zoláštni otisk z Časopisu Národního Musea, 1925, pp. 1–3.
Localities of *Belonia russula* in Czecho-Slovakia. Other lichens are also listed.

—— Nález lišajníku *Sarcopyrenia gibba* Ny. ve středních Čechách. Op. cit. 1926, pp. 1–2.
New localities for a somewhat rare lichen, *Sarcopyrenia gibba*.

—— Zur Flechtenflora des Südbanats. Verhandl. und Mitteil. Siebenbürgischen Vereins Naturwiss. Hermannstadt, lxxix, pp. 1–10 (1929).
Lichens recorded from a district on the Donau-valley lands and beech-woods.

—— Flechten aus Jugoslavien. Hedwigia, lxix, pp. 1–38, 2 figs. (1929).

—— Biometrické vyjadřování rozměrů spor. Zolastni otisk z Vědy přirodní roč, x, pp. 1–5 (1929). Slovakian.
Comparative measurements of spores of *Xanthoria parietina* from different localities.

Smith, A. Lorrain. Lichens. Encycl. Brit. Ed. 14, xiv, pp. 29–34, 11 figs. (1929).
A general account of the class Lichenes.

Stocker, Otto. Physiologische und ökologische Untersuchungen an Laub und Strauchflechten. Flora, cxxi, pp. 334–415 (1927).

Suessenguth, Karl. Zur Frage der Vergesellschaftung von Flechten mit Purpurbakterien. Ber. Deutsch. Bot. Ges. xliv, pp. 573–8 (1926).

Suza, H. H. Lichenes in A. Degen, Jul. Gayer und Josef Scheffer, Die Flora des detreköcsütörlöker Moores und des östlichen Teiles des Marchfeldes. Magy. Bot. Lapok, xxii, pp. 1–116 (1923).

In the sandy soil xerophytic lichens such as Cladoniae were abundant. These moor lichens were such as occur in Central Europe in very high regions.

—— Přispěvky k Lišejníkové Floře Vysokých Tater. (A review of the lichen flora of the Tatra.) Zvl. otisk ze Sborn. Klubu Přirodověd. Brne, ix, pp. 1–28 (1926).

A long list of lichens. Notes, localities, etc., in Slovakian.

—— Przyczynek do znajomości flory porostów Polski (Additamenta ad lichenes Poloniae cognoscendos). Acta Soc. Bot. Pol. (Livre jubilaire), v, pp. 213–19 (1928).

A considerable addition to the lichen flora of Poland. Cladoniae are especially abundant.

—— Lichenologická Exkurse na Rašeliny "Bor" v Oravské Župě na Slovensku. Zvl. otisk z Přírodov čis. xx, pp. 1–6, 2 figs. (1927).

An account is given of the lichens found on the excursion.

—— Lichenologický Ráz Západočeských Serpentinů. Der Lichenologische Charakter des Serpentinbodens in Westböhmen. (Slovakian with German Résumé.) Časopis Morav. Zemsk. Musea, xxv, pp. 1–32 (1927–1928).

—— Zajímavé nálezy lišejniků v Československu. Tom. cit. pp. 283–87 (Slovakian). A note in German states that the paper gives the results of a study of herbarium material for the whole region of the Czecho-Slovakian Republic.

Szatala, Ödön. Újabb adatok Ungmegye Zuzmóflorájának ismeretéhez. (Neue Beiträge zur Flechtenflora des Unger Komitates.) Magy. Bot. Lapok (Ungarische Botan. Blätter), xxi, pp. 33–63 (1922).

In this paper Szatala has listed 377 species from various districts of the Unger Komitates.

—— Adatok Magyarország Zúsmóflórájának ismeretéhez. (Beiträge zur Kenntnis der Flechtenflora Ungarns.) Op. cit. xxiv, pp. 43–75 (1925, 1926); II. Op. cit. xxv, pp. 201–18 (1927).

The second of these papers supplements the data published in the first and represents considerable additions to the lichen flora.

—— A Magyarországi Coniocarpineae—k Krítikai Feldolgozása. Revisio critica Coniocarpinearum Hungariae. Ann. Mus. Nat. Hung. xxiv, pp. 99–135 (1926).

A list of species recorded for Hungary from various herbaria.

—— Lichenes in Asia Minore ab directore Dre Stefano Györffy de Szigeth (Budapest) et Dre Josefo Andrasovszky collecti. Folia Crypt. Inst. Bot. Univ. litt. reg. Hung. Franc.-Joseph. i, N. 5, pp. 271–7 (1927).

A representative collection from a little known district.

—— Lichenes Hungariae. Magyarország Zúsmóflórája. I. Pyrenocarpineae—Gymnocarpineae (Coniocarpineae). Tom. cit. pp. 337–434.

A first instalment of a lichen flora for Hungary. No descriptions are given, but synonymy and localities are cited. The list comprises 250 species.

—— Neue Flechten. Magy. Bot. Lapok, xxiv, pp. 29–31 [1925] (1926).

Several new species and forms are described from Hungary.

—— Lichenes lecti a † dr. e. Pappafava in Dalmatia et in Montenegro. Tom. cit. pp. 86–7.

A short list of familiar species.

—— Eine neue Flechte der Natronböden des Ungarischen Tieflandes. Tom. cit. p. 108.

The new species described is *Catillaria* (*Biatorina*) Zsakii.

Szatala, Ödön. Adatok Magyarorszag zuzmóflórájának ismeretéhez II. (Beiträge zur Kenntnis der Flechtenflora Ungarns II.) Op. cit. xxv, pp. 201–18 [1926] (1927). Hungarian.

—— Lichenes Turciae asiaticae a Patre Prof. Stefano Selinka in insula Burgas Adassi (Antigoni) lecti. Op. cit. xxvi, pp. 18–22 [1927] (1928). Hungarian.
A list of species of which two are new to science.

—— Beiträge zur Flechtenflora der Insel Arbe. Tom. cit. xxvi [1927], pp. 27–45 (1928).
A list of 129 species from the Arbe Island (Adriatic) mostly collected by J. B. Kummerle.

—— Adatok magyarország zuzmóflórajának ismeretéhez III. (Beiträge zur Kenntnis der Flechtenflora Ungarns III.) Op. cit. xxvii, pp. 25–50 [1928] (1929). Hungarian and German.

—— Beiträge IV. Tom. cit. pp. 68–81.
A continuation of the previous paper. In both the work is based on specimens in the National Hungarian Museum at Budapest.

—— Beiträge zur Flechtenflora von Bulgarien. I. Op. cit. xxviii, pp. 82–99 [1929] (1930).
A first account of the lichenological exploration of Bulgaria by the author.

—— Enumeratio Lichenum a cl. barone G. de Andreaszky in Africa boreale lectorum. Tom. cit. pp. 162–6.
A collection of lichens from various localities in N. Africa determined by Szatala.

Szatala, O. et G. Timko. Adatok Albánia flórájához—Additamenta ad floram Albaniae. A Magyar Tudományos Akadémia Balkán-kutatásainak tudományos eredményei. III. Kölet.—Budapest, pp. 159–79 (1926).
Lichens from the Balkans and Albania, collected by J. Andrasovszky, 233 species are listed.

Tengwall, T. A. Renlavarnas tillväxt och Biologi i Torne och Lule Lappmarken. (Growth and biology of the reindeer lichen in Torne and Lule Lappmarken. With German résumé.) Svensk Bot. Tidskr. xxii, pp. 18–32 (1928).

Thaxter, Roland. Note on *Myxotheca hypocreoides* and its Synonymy. Mycologia, xix, pp. 160–4 (1927).

Tobler, F. Zur Kenntnis des Phototropismus von Cladoniapodetien und verwandten Organen. Planta, iii, pp. 169–71 (1927).

—— Zur Kenntnis der Flechtensymbiose und ihrer Entwickelung. Ber. Deutsch. Bot. Ges. xl, pp. 220–34, 1 pl. 8 figs. (1928).

Tomin, M. P. Neue Flechten aus Süd-Ost Russland, Woronesch, 1926, pp. 1–8. Russian with German summary.
A short list of lichens, four of them new to science.

—— Beiträge zur Lichenen-Flora des Gouvernements Woronesch, pp. 1–14 (*undated*). Russian with short German summary.
141 species—with one new species of *Dermatocarpon* are recorded.

—— Neue Flechten aus Süd-Ost-Russland. Natur. a. Agricult. arid reg. U.S.S.R. Woronesch, Nos. 1–2, pp. 47–52 (1927). See Ann. Mycol. xxvi, p. 468 (1928). Paper not seen.

—— Lichenes nonnulli novi Rossiae austroorientalis. Woronesch, 1929, pp. 1–5.
Three new species are described with Latin diagnoses. (Genera are *Endocarpon*, *Lecanora* and *Rinodina*.)

Vainio, Edv. A. Lichenographia Fennica. III. Coniocarpineae. Acta Soc. Faun. et Fl. Fennica, lvii, No. 1, pp. 1–138 (1927).

—— Enumeratio Lichenum in viciniis fluminis Konda (circa 60° lat. bor.) in Sibiria occidentali crescentium. Ann. Acad. Sc. Fenn. Ser. A, xxvii, N. 8, pp. 1–122 (1928).

VAINIO, EDV. A. New Species of Lichens from Porto Rico. II. Mycologia, XXI, pp. 33–40 (1929).

A previous series was published in Mycologia, XIX, pp. 206–21. The present series are crustaceous species. A new genus and species, *Finkia portoricensis*, is described.

—— Neu-Caledonische Flechten. Vierteljahrsschrift Naturf. Ges. Zürich, LXXIV, pp. 50–2 (1929).

Three new species (*Usnea spinosissima*, *Sticta ignambensis* and *Lecidea epiochracea*) are described from collections in Loyalty Island and New Caledonia.

VELENOVSKY, J. Die Flechten und unsere Bäume. Mykologia, V, pp. 65–68, 1 pl. (1928). Czech. Paper not seen.

VILLANI, A. Licheni ritrovati nel Polesine del Cav. Grigolato, Rodigino, Nuovo Giorn. Bot. Ital. XXXIV, pp. 533–7 (1927).

A series of lichens with notes as to locality and habitat, etc.

WATSON, W. Lichenological Notes—III. Journ. Bot. LXVI, pp. 17–21, 1 fig. (1928).

Records of rare species and forms with one species, *Staurothele innata*, new to science.

—— The Classification of Lichens. New Phytologist, XXVIII, I, pp. 1–36; II, pp. 85–116 (1929).

—— Lichenological Notes—IV. Journ. Bot. LXVII, pp. 74–9 (1929).

A record of new or rare lichens for Great Britain. Among the rare species are *Parmelia sorediata*, *Microglaena Breadalbanensis*, *Stenocybe bryophila* and *Thelidium terrestre*.

—— The Lichens of Somerset. Somerset Arch. and Nat. Hist. Soc. pp. 1–94 (1930).

WERNER, R. G. Sur la multiplication par conidies dans les cultures pures des Champignons des lichens. Compt. Rend. Soc. Sav. Sc. Poitiers (1926), pp. 113–15 (1927).

—— Biologie végétale.—Symbiose obligatoire ou vie indépendante des Champignons de Lichens. Comptes Rendus Acad. Sci. CLXXXV, pp. 837–9 (1927, 2).

—— Influence du milieu sur la croissance des Champignons de Lichens. Tom. cit. pp. 1149–51 (1927, 3).

—— Recherches biologiques et expérimentales sur les Ascomycètes de Lichens. Thèse présenté à la Faculté des Sci. Paris. Mulhouse Braun et Cie, pp. 1–81, 8 pls. text-figs. A to N (1927, 4).

—— Influence du milieu sur la croissance des Champignons de Lichens. Comptes Rendus Acad. Sci. Paris, CLXXXV, pp. 1149–51 (1927, 5).

—— Étude de la famille des Gyrophoraceae. Op. cit. CLXXXVI, pp. 1367–8 (1928).

—— Étude biologique et physiologique du *Celidium stictarum* (de Not.) Tul. Bull. Soc. Mycol. France, XLIV, pp. 194–205, 2 pls. (1928).

WILLIS, H. G. Lichens. Ann. Rep. and Trans. Manchester Microscop. Soc. pp. 1–18 (1928).

The writer has reviewed all aspects of lichen plants: history, structure, physiology, etc.

YASUDA, A. Flechten Japans. Sendai, 1925, 1–126, 25 pls. (Japanese). See Bot. Centralbl. 1928, CLV, p. 120 (1928).

ZAHLBRUCKNER, A. Additamenta ad Lichenographiam Japoniae. Botanical Mag. Tokio, XLI, pp. 313–64, 2 pls. (1927).

A list of 208 species is given, many of them new to science.

—— Schedae ad Kryptogamas exsiccatas. Ann. Naturhist. Mus. Wien. Lichenes, pp. 60–6 (1928).

Two decades of lichens, nos. 3051–70 are here listed. Several species are new to science.

—— Neue und ungenügend beschriebene javanische Flechten. Ann. Crypt. Exotique, I, pp. 109–212 (1928).

ZAHLBRUCKNER, A. Die Gattung *Lecanora*. Report of the Scientific Results of the Norwegian Expedition to Novaya Zemlaya, 1921, N. 44. Det Norske Vidensk. Akad. Oslo, pp. 1–32, 4 pls. (1928).

—— New Species of Lichens from Porto Rico. III. Mycologia, XXII, pp. 67–79 (1930).

The continuation of previous work by Zahlbruckner on the lichens collected by the late Professor Fink in Porto Rico. The species, 22 in all, are crustaceous with the exception of a *Ramalina* and an *Usnea*.

ZAHLBRUCKNER, A., K. KEISSLER and H. H. ALLAN. The Epiphyllous Lichens of Kitchener Park, Feilding, New Zealand. Trans. N.Z. Institute, LIX, pp. 304–14 (1928).

ZSCHACKE, HERMANN. Die Mitteleuropaischen Verrucariaceen, V, 4, *Verrucaria*. Hedwigia, LXVII, pp. 45–85 (1927).

—— Korsische Flechten gesammelt in den Jahren 1914–16. Verhandl. Bot. Ver. Brandenburg, LXIX, pp. 1–29 (1927).

An account of 204 species of lichens, 18 new to science, collected by the author during his retention as war prisoner in Corsica.

—— Neue Kernfrüchtige Flechten. Fedde, Rep. Spec. nov. XXIV, pp. 348–58 (1928).

In this paper Zschacke gives Latin diagnoses of the Verrucariae published by him in Hedwigia.

THE EXISTENCE OF PHYSIOLOGIC FORMS OF WHEAT STEM RUST IN AFRICA.

By J. McDonald, D.F.C., B.Sc., F.L.S.

(With Plate VIII and one Text-figure.)

LARGE areas of the highlands of Kenya Colony have been shown to be suitable, from the point of view of soil and climate, for the production of wheat, the limiting factor in the past having been the prevalence and severity of attack by rust. Three species of rust fungi on wheat occur in the colony, namely stem rust (*Puccinia graminis Tritici* Eriks. and Henn.), yellow rust (*P. glumarum* Eriks. and Henn.) and orange leaf rust (*P. triticina* Eriks.). The first and last occur in all the wheat areas of the country, but yellow rust is fairly sharply confined to altitudes of 7000 feet and over. Orange rust, which attacks only the leaves and leaf sheaths, undoubtedly reduces yields to a certain extent when the amount of infection is considerable, but it does not completely destroy the crop, whereas both stem rust and yellow rust are capable of doing so. Stem rust, however, having a much wider distribution, presents the greater problem.

Breeding work, especially with a view to the production of wheat varieties resistant to rust, has been in progress in Kenya for a number of years and, as a result, the present Plant Breeder was able to develop, by means of field selection, a new variety,

amongst others, which was named Kenya Governor. This wheat, which combined a number of desirable qualities and appeared to possess a high degree of resistance to stem rust, was issued to farmers and gave fair satisfaction for some time. Eventually, however, occasional instances occurred which threw doubt on its reputation for resistance to stem rust and, in fact, in one area a field of two hundred acres of Kenya Governor was destroyed by it (1). These occasional departures from what was believed to be the normal behaviour of Kenya Governor towards stem rust naturally required some explanation and, in view of knowledge gained in America of the existence of physiologic forms of stem rust, attention was turned in this direction.

Stakman and Piemeisel (8) first showed the existence of physiologic forms within the biologic species *Puccinia graminis Tritici*, and since then the discovery of numerous other physiologic forms of the rust in the American continent and Australasia has followed (4, 5, 9, etc.), until at present the total of such known forms is well over fifty. These discoveries offered a possible explanation of the variable behaviour of Kenya Governor towards stem rust in Kenya Colony, and since it was realised that the knowledge of the existence of different physiologic forms would have an important bearing on future work on wheat breeding in the country, a systematic investigation to discover whether more than one such form was present was begun at Nairobi in 1927.

Methods.

As no greenhouse accommodation was available it was necessary to make some preliminary experiments to discover other suitable means of combining the conditions necessary to successful artificial infection experiments, while providing protection from adverse climatic conditions. Nairobi is little more than one degree south of the equator and it was soon found that difficulties due to geographical situation had to be overcome.

Fromme (2) working with *Puccinia dispersa* and *P. coronifera*, Stakman (6) using *P. graminis*, and others have shown that optimum conditions for rust infection include humidity approaching saturation, a considerable degree of illumination and a suitable temperature. Stakman found that the last appeared to range between 66·5° and 70° F.

Early experiments in which pots of wheat seedlings of known susceptible varieties, kept in small muslin cages on a roofed verandah, were inoculated with uredospores of *P. graminis* and placed under bell-jars for the first forty-eight hours, produced only feeble infection. This failure was attributed largely to lack of sufficient illumination, but since, on one occasion, a maximum

temperature of 102° F. was recorded inside a cage, the temperature factor may also have been important. After further experimentation, the following arrangement was found to work satisfactorily and was finally adopted.

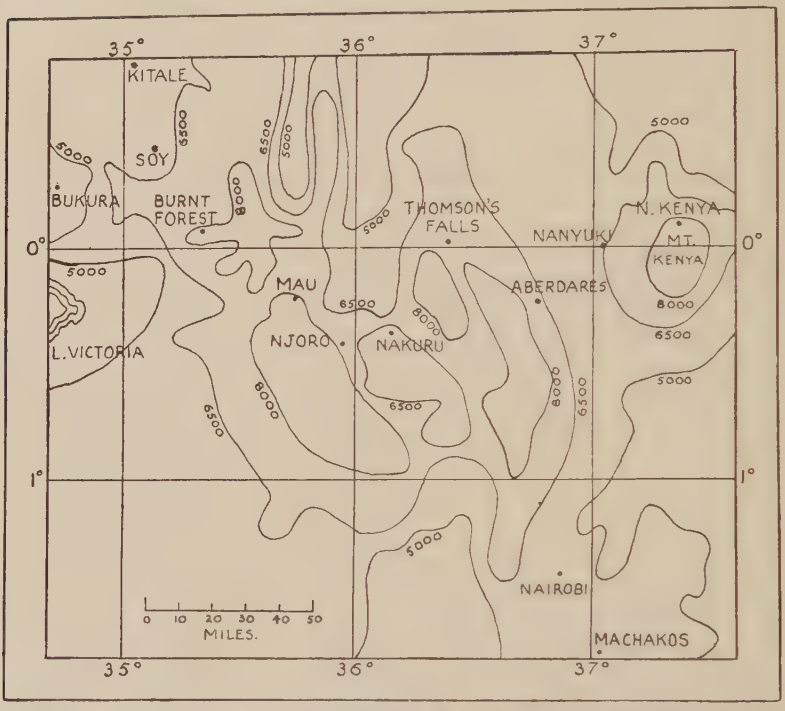
A number of cages approximately eight feet long, seven feet high and six feet wide, consisting of a wooden framework, covered on top and on all sides with butter muslin, and having a tightly fitting door covered with the same material, were constructed and placed in a row in such a position that they were sheltered from the prevailing wind, first by an avenue of trees, then by a screen of "buffalo" grass and finally by a palisade of split bamboo. Overhead shade, which could be varied as occasion demanded, was provided by means of further lengths of split bamboo laid from front to back across the top. These also served to support sheets of galvanised iron, which were placed over the cages at night and at other times when necessary to protect against rain.

Throughout the investigations, after the preliminary experiments were concluded, all inoculations were normally carried out on seedlings raised in six- or eight-inch pots, planted ten seeds per pot. The inoculum of uredospores of *P. graminis* was applied near the tips of the leaves of seedlings ten days old, by means of a flat needle, care being taken to avoid mechanical injury of the epidermis. In each of the first thirty or so experiments, in order to test the efficiency of the cages and the methods used, an uninoculated control pot, containing ten seedlings of a known susceptible variety, was included. Throughout this period, a single rust pustule only on each of two leaves was found in the control pots and it was therefore considered unnecessary to continue to include them.

At the end of 1927 and during the growing season of 1928, collections of stem rust were obtained from as many districts as possible. Such samples were thus obtained from Nairobi, Machakos, Nanyuki, Aberdares, North Kenya, Njoro, Molo, Burnt Forest, Soy and Kitale districts. It will be seen from the accompanying sketch map (Text-fig. 1) that these districts are spread over a large area and embrace a wide range of altitudes. Nothing was known, of course, at first of the suitability of the available wheat varieties as differential hosts. Each of the rust collections was therefore used to inoculate a number of named varieties grown locally by farmers, numerous unnamed hybrid selections obtained from the Plant Breeder and the whole series of twelve varieties employed as differential hosts in America. The last were obtained through the courtesy of Dr M. N. Levine of Minnesota. The reactions of the various wheats were recorded twenty-one days after inoculation and according to the scale of

values devised by Stakman and Levine (7) for the identification of physiologic forms occurring in America. The records thus obtained were carefully watched for any variations which might occur between the results obtained with the different rust samples.

When these experiments had been in progress about six months, it was observed that two wheat varieties gave different reactions when inoculated with rust from samples which had



Text-fig. 1. Sketch map of the highlands of Kenya Colony showing position and approximate altitude of localities from which rust collections were obtained.

been obtained from Nairobi and Njoro respectively. The two varieties exhibiting these differences were Kenya Governor and Einkorn, the latter of which is one of the American differential hosts. Kenya Governor proved to be moderately susceptible to the Nairobi rust and highly resistant to that from Njoro, while Einkorn reacted in an opposite manner in each instance, that is to say, it showed moderate susceptibility where Kenya Governor was highly resistant and *vice versa*.

The inoculations with the rust samples from the two different

sources had been carried out at slightly different times and in different cages. In order, therefore, to confirm the observations made, a special experiment was designed to make the tests under identical conditions.

Two batches each of Kenya Governor and Einkorn seedlings were raised simultaneously in the same cage, in pots of soil from the same source. When these seedlings were ten days old, one set of seedlings of each variety was inoculated with rust from the Nairobi source and the other set with that originally from Njoro. While one set of seedlings of each variety was being inoculated with the Nairobi rust, the remaining set was carefully protected by a bell jar, the same procedure being adopted with the first set while the second was being inoculated with the Njoro rust. To ensure uniformity in the inoculum used, this was obtained from two pots of seedlings of Spelmar wheat of the same age which had been previously inoculated on the same day with Nairobi and Njoro rust respectively. The Spelmar variety had been chosen for the purpose because it was known to be equally and highly susceptible to the rust from both sources. The bell-jars were left over the Kenya Governor and Einkorn seedlings for the usual period of forty-eight hours and the results of the inoculations were observed twenty-one days after they were carried out. It was then found that as a result of the inoculation with the Nairobi rust, a moderate number of pustules of medium size had developed on the leaves of Kenya Governor while a few minute sori only had appeared on some of those of Einkorn, the remainder of which showed mere flecks without sori as evidence of infection. Inoculation with the Njoro rust on the other hand produced an opposite result in both instances. The whole experiment was repeated with almost exactly similar results. The reactions obtained in the two experiments are given, according to Stakman and Levine's scale (7), in Table I.

Table I. *Reactions of Kenya Governor and Einkorn wheat varieties when inoculated under uniform conditions, with* Puccinia graminis Tritici *obtained from two different localities.*

Variety		Rust from Nairobi	Rust from Njoro
Kenya Governor	1st experiment	3	1 =
	2nd experiment	3	0
Einkorn	1st experiment	1 =	4 −
	2nd experiment	1 =	3 +
Physiologic form		K 1	K 2

The rust collections used in the experiments so far described were obtained from localities over a hundred miles apart and

differing in altitude by 1400 feet. In order to meet any possible criticism on these grounds, a similar experiment was conducted at Njoro, using as sources of inoculum infected leaves taken from the cages at Nairobi. The result was essentially the same; the type of infection produced corresponded with that at Nairobi with each variety of wheat inoculated with the respective rusts, but there was a slight depression in the degree of infection, *i.e.* in the number of pustules produced. This, however, was to be expected since, owing to the difference in altitude, the host seedlings developed less vigorously at Njoro than at Nairobi.

As a result of the foregoing experiments, it was definitely concluded that at least two different physiologic forms of *Puccinia graminis Tritici* exist in Kenya Colony. The two forms discovered are now designated K 1 and K 2 respectively, the former producing the reactions given in Table I for Nairobi rust and the latter those for Njoro rust. It will be shown later, however, that the forms are not constant for particular localities. The types of reaction produced on Kenya Governor seedlings by forms K 1 and K 2 respectively are shown in the photograph (Pl. VIII).

It is confidently believed that this constitutes the first proof of the existence of different physiologic forms of *Puccinia graminis Tritici* in the African continent.

It was considered of interest to discover whether any significant difference exists between the uredospore dimensions of the two forms. For this purpose, two pots of seedlings of Spelmar wheat were grown simultaneously in the same cage and in soil from the same source. Each batch of seedlings was inoculated at ten days old with each of the two rust forms respectively. On the twenty-second and twenty-third days after inoculation, length and breadth measurements were made of both forms, an equal number of each being made on each day. The total number of spores measured was two hundred of each form, *i.e.* a grand total of eight hundred measurements. In addition, an exactly similar procedure was later carried out except that Little Club wheat was used instead of Spelmar. Both these wheats are congenial hosts for both rust forms. The statistical results of these experiments are presented in Table II, from which it will be seen that a decidedly significant difference exists between the mean lengths of the uredospores for each form on both host varieties. A barely significant difference was found for the mean widths on Spelmar but the difference on Little Club was not significant. The data for the spore lengths, however, provide an additional proof, if such were needed, that forms K 1 and K 2 do actually differ from each other.

During the period of over two and a half years since the

Leaves of seedlings of the wheat Kenya Governor inoculated with form K 1 (left) and form K 2 (right) of *Puccinia graminis Tritici*.

present investigation was begun, frequent opportunities have been taken at various times of testing stem rust material from different districts. The main object of these tests has been the discovery of further physiologic forms, but, at the moment of writing this account (April, 1930), only the two already described are known to exist in Kenya Colony. A second object which has been kept in view, however, has been the collection of information on the possible seasonal distribution of the two forms or

Table II. *Dimensions in microns of uredospores of* Puccinia graminis Tritici, *forms K 1 and K 2, grown on two congenial hosts, Little Club and Spelmar, under uniform environmental conditions.*

		Spore classes												
Host	Form	15	17	19	21	23	25	27	29	31	33	35	37	39	41
LENGTHS:															
L.C.	K 1					3	8	17	26	28	49	40	25	3	1
	K 2				3	8	12	27	35	71	31	12	1		
Spelmar	K 1						5	12	18	37	68	32	21	7	
	K 2				2	15	27	44	48	39	15	8	2		
WIDTHS:															
L.C.	K 1	2	8	46	125	19									
	K 2	1	18	35	122	24									
Spelmar	K 1		30	35	111	24									
	K 2	6	31	74	80	9									

Host	Form	Size limits	Means	S.E.	Standard deviation	Diff. of means.	S.E.	No. of readings
LENGTHS:								
L.C.	K 1	21·9–40·2	32·25	± 0·26	3·72	2·39	± 0·34	200
	K 2	20·7–36·6	29·86	± 0·22	3·09			200
Spelmar	K 1	24·0–39·0	32·66	± 0·22	3·07	4·10	± 0·32	200
	K 2	20·7–36·1	28·56	± 0·23	3·27			200
WIDTHS:								
L.C.	K 1	15·4–23·1	20·51	± 0·10	1·44	0·04	± 0·15	200
	K 2	15·0–23·6	20·47	± 0·11	1·61			200
Spelmar	K 1	16·2–23·6	20·29	± 0·12	1·75	0·74	± 0·18	200
	K 2	15·0–23·1	19·55	± 0·12	1·77			200

their correlation with altitude. The wide range of altitude, approximately 4500 to 9000 feet, over which wheat is grown in Kenya appeared favourable for such a study. In most districts material for testing has been available only through the courtesy of wheat farmers, so that it has usually been impossible to obtain rust samples except at those periods of the year when the crops have been in the necessary stage of maturity. Climatic conditions have also been a controlling factor in the investigations, and in 1929 were generally so unfavourable for stem rust, that the disease was almost or entirely absent over large areas of the

country. At Nairobi and Njoro, where there are Government experimental stations, wheat crops in various stages of development have existed during a greater portion of each year than elsewhere and have made possible a larger number of tests of rust from those places than from other localities.

Table III.

Locality	Altitude in feet	Date when rust collected	Form present
Nairobi	5700	Dec. 1927	K 1
		Oct. 1928	K 1 and K 2
		Feb. 1929	K 2
		Apr. 1929	K 2
		June 1929	K 2
		Aug. 1929	K 1
		Jan. 1930	K 1
Njoro	7100	Feb. 1928	K 2
		Sept. 1928	K 1
		Nov. 1928	K 1 and K 2
		Sept. 1929	K 1
Mau	8500	Jan. 1928	K 2
		Jan. 1929	K 2
		Jan. 1930	K 2
Thomson's Falls	7700	Feb. 1929	K 2
		Jan. 1930	K 2
Machakos	5400	July 1928	K 1
		Aug. 1929	K 1
North Kenya	8500	Aug. 1928	K 2
Nanyuki	6500	Aug. 1928	K 1 and K 2?
Aberdares	7000	Aug. 1928	K 1
Kitale	6200	Oct. 1928	K 1
Soy	6400	Oct. 1928	K 1
Burnt Forest	8000	Nov. 1928	K 1
Nakuru	6100	Jan. 1929	K 1
Bukura	4600	Dec. 1928	K 1

The results of twenty-six tests of rust collections, obtained at different times from widely separated localities (Text-fig. 1) and covering an altitude range of nearly 4000 feet, are given in Table III. The table shows that, including the somewhat doubtful result with the rust from Nanyuki, form K 1 occurred sixteen times and form K 2 thirteen times. The average altitude of all the localities from which rust samples were obtained is 6700 feet. Taking this as a convenient dividing line between the higher and lower altitudes, certain interesting comparisons can be made, although for obvious reasons no definite conclusions can be drawn from them. It will be seen that form K 1 was found eleven times at the lower, and only five times at the higher altitudes, while form K 2 was found more often at the higher altitudes than at the lower, the figures being eight and five times respectively. Another fact which emerges is that form K 1 has not yet been recorded at either of the two highest localities, nor form K 2 at either of the two lowest.

Comparison of forms K 1 and K 2 with American physiologic forms.

Stakman and Levine (7), in compiling their dichotomous key to American physiologic forms, group together their infection types 0, 1 and 2 as resistant and types 3 and 4 as susceptible. If the same procedure is adopted for the two Kenya forms, the reactions which they produce on the twelve American differential hosts are as given in Table IV. One of the hosts, Kanred, a winter wheat, takes so long to mature under Kenya conditions that some difficulty was experienced in maintaining a supply of seed of this variety. On hearing of this, Dr Levine was good enough to send seed of a thirteenth variety, a spring wheat named Reliance, which he had found to give the same reactions as those of Kanred. Reliance is therefore also included in Table IV, from which it will be seen that it gives the same reactions as Kanred with the Kenya forms also.

Table IV. *Reactions produced on American differential hosts by Kenya physiologic forms, K 1 and K 2.* (R. = resistant, S. = susceptible.)

Variety	Form K 1	Form K 2
Kanred	R.	R.
Reliance	R.	R.
Vernal (White Spring Emmer)	R.	R.
Khapli	R.	R.
Einkorn	R.	S.
Kota	S.	S.
Acme	S.	S.
Arnautka	S.	S.
Mindum	S.	S.
Kubanka	S.	S.
Marquis	S.	S.
Little Club	S.	S.
Spelmar (Speltz Marz) ...	S.	S.

By the use of Stakman and Levine's analytical key, it will be found that Kenya form K 1 produces reactions corresponding to those of American form 21 while the reactions to Kenya form 2 are the equivalent of those of American form 17. In order to obtain further evidence on the likelihood or otherwise that the two Kenya forms are actually identical with the respective American forms it was considered desirable, if possible, to compare the spore measurements. Unfortunately those for American form 21 have not so far been obtainable. Levine, however, has published (3) the necessary length and width measurements for American form 17 which, he states in a letter to me, were obtained from infections on Little Club. His data are collected in Table V. A comparison between the data given in Table II for

uredospores of Kenya form K 2 on Little Club and Levine's figures for American form 17 on the same host, show a very close resemblance in the distribution of the spore classes, the size limits and, especially, in the means. It seems reasonable to believe, therefore, that the two forms are in fact identical. In comparing the figures for size limits, it should be borne in mind that the Kenya spore sample was twice as large as that for the American form.

Table V. *Dimensions in microns of American form* 17 *on Little Club.* (Figures taken from Levine (3).)

	Spore classes										Size limits	Means	P.E.	Standard deviation P.E.	No. of readings
	21	24	27	30	33	36									
Lengths	1	7	26	40	24	2					22·08–36·57	29·55 ± 0·19		2·89 ± 0·14	100
	16	17	18	19	20	21	22	23	24						
Widths	1	1	4	16	36	30	10	1	1		16·10–24·38	20·26 ± 0·08		1·20 ± 0·06	100

Arising out of the foregoing comparisons the suggestion is put forward that it might be possible to standardise the physiologic forms of wheat stem rust existing throughout the world. By determining the reactions on a standard set of host varieties, and supplementing the information thus obtained by statistical data of spore measurements, it is considered that the identity of forms in different parts of the world could be established with some confidence. The twelve American differential hosts are thoroughly established varieties and might well serve as the basis for standardisation, although it is possible that new forms will be found which may require an extension of the host range to enable them to be distinguished from forms already known to exist. If the identity of forms in different countries were reasonably well known, and if the reactions of the most promising wheat varieties in each country were recorded, the information could be used in connection with the exchange of varieties between countries in which the same forms exist. Much time and labour at present expended in importing and testing varieties useless from the point of view of rust resistance, could thus be saved.

Routine testing of new varieties.

Since the discovery was made that two different physiologic forms of stem rust exist in Kenya, the testing of the Plant Breeder's new hybrid selections in the seedling stage by artificial inoculation with both forms of rust has been adopted as a matter of routine. While it is recognised that seedling inoculations are not a completely infallible guide to the behaviour of varieties towards rust infection at all stages of growth, the method has

proved of considerable value. As a general rule, it has been found that the results obtained under the conditions obtaining in artificial inoculation tests indicate the extreme degree of infection which varieties are likely to exhibit under the most favourable conditions for rust in the field. Such tests therefore serve to avoid the necessity of growing new hybrid selections for an indefinite number of seasons until conditions favourable for a severe rust test chance to occur. The Plant Breeder has thus been enabled to eliminate, at an early stage, a large proportion of new hybrids which have failed to exhibit a promising degree of resistance to stem rust when tested by artificial inoculation.

The routine testing carried out has served to emphasise several points of interest. The number of rust pustules produced has been found to be of much less importance than their size and appearance. Within wide limits the amount of inoculum used, provided it is at least a reasonable quantity, has little effect on the number of rust pustules subsequently produced. Reduction of illumination, however, has a depressing effect on the amount of rust resulting from inoculation. Thus, if inoculations are carried out during dull weather, fewer pustules may be produced than would have been the case under better light conditions. If, however, even a single elongated pustule of moderate size, but devoid of a surrounding hypersensitive area be produced, the resistance of the variety is at once open to doubt. On the other hand, the occurrence of quite numerous pustules, provided they are small and surrounded by hypersensitive areas, does not indicate that the variety will prove susceptible in the field.

The system of routine testing has been of value in detecting selected lines which were believed, on the evidence of field observations, to have reached a state of purity for rust resistance but which actually had not done so. Batches of such seedlings, under artificial inoculation, disclose their mixed character by the different types of infection which the individual plants exhibit.

The author desires to express his gratitude to Mr A. Holm (Director of Agriculture, Kenya Colony) for much encouragement and assistance, to Dr M. N. Levine of Minnesota for supplying seeds of the American wheat varieties used, and to Mr G. J. L. Burton (Plant Breeder) for assistance in the collection of rust samples and for helpful discussion in connection with these investigations.

Summary.

1. Three rusts attack wheat in Kenya Colony of which stem rust (*Puccinia graminis Tritici*) is the most destructive and constitutes the chief obstacle to successful wheat growing.

2. Plant breeding work in the past led to the production of a new wheat variety, Kenya Governor, which was at first thought to combine high resistance to stem rust with other desirable characters. In course of time, however, this variety was found on occasion to be severely attacked by stem rust. An explanation of this was sought by means of an investigation to discover whether more than one physiologic form of stem rust exists in Kenya Colony.

3. The methods used in the investigation are described and the discovery of the existence of two physiologic forms is recorded. Details of proof are given by reference to the different reactions which the forms respectively produce on certain wheat varieties used as differential hosts. The two forms may also be distinguished on the basis of their uredospore dimensions.

4. The records of tests carried out with twenty-six stem rust samples obtained at various times from localities ranging in altitude from 4600 to 8500 feet, suggest that one form tends to occur more commonly at the higher, and the other form at the lower altitudes.

5. The forms have been designated K 1 and K 2 respectively. They have each been tested by inoculation on all the twelve American differential host varieties and, as a result, it is shown that the reactions which they produce correspond with those of American forms 21 and 17 respectively. A comparison of uredospore measurements of Kenya form K 2 and American form 17 strengthens the impression that the two are probably identical. Arising from this, the suggestion is put forward that it might be possible to achieve a measure of standardisation of forms of stem rust throughout the world, as a guide in connection with the interchange of wheat varieties.

6. The advantages derived from a system of routine testing of new hybrid selections by artificial inoculation with the two physiologic forms are discussed.

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EXPLANATION OF PLATE VIII.

Leaves of Kenya Governor seedlings inoculated, left, with form K 1 and right, with form K 2.

REVISIONS OF CEYLON FUNGI, PART IX*.

By T. Petch, B.A., B.Sc.

380.—*CLAVARIA FUSCO-LILACINA* Berk.

THIS species has been recorded from Java by van Overeem in *Icones Fungorum Malayensium*, and his figures strongly resemble the Ceylon species which has been described as *Clavaria xylarioides* Petch. The type of *Clavaria fusco-lilacina* in Herb. Kew contains one specimen only. It is a dense cluster of stout clavae (or branches) which appear to arise from a common base, but it is possible that they may be merely united at ground level by mycelium. The branches divide once or twice from about half their height, and together form a loosely coralloid fructification. The colour is now pale purple-brown. The specimen is quite different from van Overeem's figures and description, and the Javan species is certainly not *Clavaria fusco-lilacina*.

381.—*ANGELINA LEPRIEURII* Mont.

This was recorded for Ceylon by Berkeley and Broome in *Fungi of Ceylon*, No. 1148, as follows:

"1148, *Angelina Leprieurii* Mont. Syll. p. 188 (nos. 6, 362, 1066). On wood, etc., Central Province, etc., Dec. 1868."

"No. 1066 is on a confluent *Sphaeria*. Sporidia ·0012–·0015 long by ·0005. Varying in the degree in which it is transversely striate, and in the size of the sporidia."

Angelina Leprieurii Mont. is *Tryblidiella Leprieurii* (Mont.) Sacc.

Herb. British Museum has Thwaites 6, marked "spores ·0015

* Continued from Annals of the Royal Botanic Gardens, Peradeniya, X, p. 180.

long, ·0005 w." and Thwaites 1066, marked "spores ·0012 × ·0005 w."

Herb. Kew has numerous sheets and drawings of Thwaites 6, 362, 1066. 362 is marked by Thwaites, "comp. with 6, but in 362 the hymenium is differently coloured." As noted in *Ann. Perad.* VII, p. 27, the disc is usually reddish brown to olive, but sometimes greenish yellow.

In Thwaites 6, the lips are strongly transversely grooved, and the spores measure 30–36 × 10–12 μ.

In Thwaites 362, the lips are again strongly transversely grooved, but the spores are 20–30 × 8–9 μ in the specimen in Herb. Peradeniya.

In Thwaites 1066, the lips are not grooved, and the spores measure 26–32 × 8–12 μ.

In Herb. Kew, all the Ceylon specimens are now labelled *Hysterium rufulum* Spreng., which is *Tryblidiella rufula* (Spreng.) Sacc.

Montagne (*Syll. Crypt.* p. 188) described *Angelina Leprieurii* as having "labiis fuscis longitrorsum tenuissime striatulis," and spores, 30 × 10 μ, fuscous, three-septate. *Angelinia* Fries (now *Angelina*) has hyaline, one-septate spores, and Montagne's species was therefore transferred to *Tryblidiella*. Saccardo (*Syll. Fung.* II, p. 758) gave the dimensions of the spores as 32–40 × 10–12 μ.

Tryblidiella rufula has the lips transversely striate, and its spores, *fide* Saccardo, *loc. cit.*, are 30–35 × 10 μ.

In none of the Ceylon specimens referred to above are the lips longitudinally striate. In two, the lips are transversely striate, but, while in one the spore measurements agree with those recorded for *Tryblidiella rufula*, in the other they are much smaller. In the third specimen, the spores nearly agree with *Tryblidiella rufula*, but the lips are not striate.

It would appear probable that, as Berkeley and Broome decided, these variations do not amount to specific differences, and that these Ceylon collections should all be referred to *Tryblidiella rufula*.

382.—*Pseudohelotium hyalinum* (Pers.) Fuck.

In *Fungi of Ceylon*, No. 908, Berkeley and Broome recorded *Aegerita candida* P., Thwaites 285 and 349; and in *Fungi of Ceylon*, No. 949, *Peziza* (*Dasycyphae*) *hyalina* P., Thwaites 285 in part, on dead wood with *Aegerita candida*.

Part of Thwaites 285 is in Herb. Peradeniya; it contains only the *Aegerita*. There is no Ceylon specimen of either *P. hyalina* or *Aegerita candida* in Herb. British Museum. In Herb. Kew, in the cover of *Aegerita candida*, are a sheet with a Thwaites

label, "No. 285 and 349, Central Province, Ceylon, Dec. 1868," marked *Aegerita candida* by Berkeley, a drawing of the *Aegerita* marked "Ceylon 349," and another sheet marked by Berkeley, "*Aegerita candida* and *Peziza hyalina*, 285 Ceylon, G.H.K.T." In the cover of *Pseudohelotium hyalinum* in Herb. Kew, there is a specimen which bears a Thwaites label, "No. 285, Peziza?, very minute, white," marked *Peziza hyalina* by Berkeley; there is no drawing of the *Peziza*.

There does not appear to be any *Peziza* on these specimens. All the fungi are *Aegerita*. The latter varies, being sometimes white, sometimes hyaline. *Pseudohelotium hyalinum* should be deleted from the Ceylon list. The *Aegerita* has been re-described as *Aegerita discoidea* Petch in *Ann. Perad.* x, p. 168.

383.—*Stachybotrys asperula* Massee.

This species was described by Massee in *Grevillea*, xvi, p. 26, as "Effusa, atra. Hyphis gregariis, repentibus, furcato-ramosis, assurgentibus, granulato-asperulis, sterigmatibus clavatis, capitato-coronatis, conidiis globosis, asperulis (7–10 μ), atrofuscis, opacis. In company with Chaetomium. On damp paper from Ceylon, Kew."

The *Stachybotrys* is loose, spreading, effused, or in minute tufts, subsequently coalescing in large black patches. The hyphae are hyaline to fuliginous, 4 μ diameter, minutely verrucose. The conidiophores are fuliginous, branched, the branches solitary or opposite, and the conidiophore sometimes inflated at the point of origin of the branches. The branches are 36–45 μ long, 3 μ diameter at the base, tapering upwards to 2 μ, and bearing at the apex a cluster of short ovate phialides, 8–12 × 4–5 μ. The conidia are catenulate, black, strongly verrucose, oval, 8–12 × 5–8 μ, or globose, 8–10 μ diameter. This does not appear to agree with any of the other species of *Stachybotrys* described from the same substratum.

The greater part of the type consists of greenish olive patches of mycelium, about 1 mm. in diameter, often confluent, consisting of closely flexuose hyphae, in the centre of each of which is a group of two or three perithecia. These perithecia are for the most part broken. As far as can be determined, they are globose, 0·1–0·2 mm. diameter, purplish, iridescent, with a thin, brown, cellular wall, glabrous above, not ostiolate, clothed below with long, spreading hyphae. These hyphae are of two kinds, the one 4 μ diameter, closely and minutely verrucose, the other smooth, 2·5–3 μ diameter, both arising from the wall of the perithecium. The ascospores are dark brown, subglobose, or oval and slightly apiculate, 9–10 × 6–7 μ. This fungus appears to be a *Chaetomidium*.

384.—*Stilbum erythrocephalum* Ditm.

Berkeley and Broome recorded this species in *Fungi of Ceylon*, No. 868. The specimen was said to be Thwaites 174, on dung, spores 0·00016 (inch) long. They added "No. 158 has globose spores 0·00015–0·0002 in diameter; but is possibly only a variety."

Thwaites 174 is represented in Herb. Kew and Herb. Peradeniya. The fungus is not on dung, but on wood and bark, possibly of *Hibiscus*. The synnemata are up to 0·6 mm. high, with a smooth, or white-pruinose, stalk, 0·1–0·15 mm. diameter at the base, equal or attenuated upwards, expanding into a flattened globose head, 0·25–0·5 mm. diameter (without the conidia). The head is now dull yellow. The basidia are about 24 μ long, 1·5 μ diameter below, attenuated upwards, and the conidia narrow-oval or oblong-oval, 3·5–5 × 1·5–2 μ, minutely granular. This does not appear to be *Stilbum erythrocephalum*.

Thwaites 158 is included in the cover of *Stilbum erythrocephalum* in Herb. Kew. It is accompanied by a drawing which shows an oval head and angularly globose conidia. This specimen is on dung (rat?). I was unable to find any synnemata bearing *Stilbum* heads. The specimen bears white, tomentose strands, up to 1·2 mm. long, 0·1 mm. diameter at the point of origin, attenuated towards the extremity and terminating indefinitely in a pencil or film. These appear to be strands of mycelium, not *Stilbum* stalks.

Stilbum erythrocephalum should not be included in the Ceylon list on the evidence of these two specimens.

385.—*Tuber zeylanicum* B. and Br.

This was described by Berkeley and Broome in *Fungi of Ceylon*, No. 975, as "Minutum, luteum rugosum, centro affixum (No. 1013). On a piece of dead stick. Peradeniya, Dec. Only a single specimen found 1½ line across, unfortunately without perfect fruit. No. 1093 is in the same condition."

Reference was made to the fact that this species is a sclerotium in *Ann. Perad.* IV, p. 439, and the name *Sclerotium zeylanicum* was used in various reports, etc., *e.g.* in the *Preliminary list of the diseases of cultivated plants in Ceylon*, Bulletin No. 52, Department of Agriculture, Ceylon (1922), but it was unfortunately overlooked that no formal correction had been published.

The fungus was re-described as *Sclerotium zeylanicum* (B. and Br.) Petch, in *The Diseases of the Tea Bush* (1923), p. 212, the description there given being, "Sclerotia produced on fleecy, white, superficial patches of mycelium overrunning plants or soil, white, then pale ochraceous or pinkish, finally brown,

glabrous, globose, about 1 mm. diameter, internally white, hard, compact."

This fungus was very common at Peradeniya from 1905 to 1910, usually on rubbish heaps, or among the dead leaves, etc. at the base of a hedge, or in flower beds, or on logs in wood piles. It is probably less common at the present day, as the smaller fungi which grow on the ground, or on sticks and dead leaves, are comparatively scarce there now, owing to the fact that they are devoured by the prevalent Kalutara snail (*Achatina fulica*). It formed conspicuous white patches, up to nine inches or more in diameter, spreading over the soil or dead leaves, on which the sclerotia were ultimately produced. On patches on the ground the sclerotia were usually more or less uniform in size, but, in some instances, especially on logs, the size varied considerably, some attaining a diameter of 5 mm. These larger specimens were single sclerotia, not aggregations of small sclerotia.

Berkeley and Broome's specimen of *Tuber zeylanicum* is one of these larger sclerotia, and, as noted by them, it grew on a stick. Small examples, of the more usual size, were included with *Sclerocystis coremioides* in Thwaites 155, and hence *Tuber zeylanicum* and *Sclerocystis coremioides* were considered identical (*Ann. Bot.* XXII, pp. 116, 117; *Ann. Perad.* IV, p. 439; *ibid.* V, p. 282). But Thwaites 155 was a mixture, and the real *Sclerocystis coremioides* is a different species. Other small examples were included with *Onygenopsis diplocystis* (B. and Br.) Petch in Thwaites 291.

As previously recorded (*Ann. Perad.* IV, p. 439), the larger examples (*Tuber zeylanicum*) when planted in damp sand, produced a white mycelium which subsequently developed small sclerotia.

In the majority of its occurrences noted by me, *Sclerotium zeylanicum* was undoubtedly merely saprophytic. When, however, the spreading mycelium came in contact with Caladiums, the latter speedily succumbed.

In the *Review of Applied Mycology*, VI, p. 390, the wording of the review suggests that this fungus is rare in Ceylon. It is only rare as regards its recorded attacks on tea; the fungus is, or was, very common. If it is identical with *Sclerotium Rolfsii*, as has been claimed, the name *Sclerotium zeylanicum* has priority.

386.—Ceylon Polyporaceae.

In a paper on "The Polyporaceae of New Zealand" (*Trans. N.Z. Institute*, LVIII, pp. 202–250) Cunningham has published several details concerning Ceylon species.

On p. 217, he states "Lloyd's *F. annularis* and *F. Petchii* are only forms of this species," *i.e. Fomes australis*. As stated by me

in *Ann. Perad.* VI, p. 133, *Fomes annularis* is a form of *Fomes applanatus* (or *australis*), but *Fomes Petchii* cannot be assigned to that species. *Fomes Petchii* has the typical upper surface and colour of *Fomes lucidus*, and was sent to Lloyd as a perennial form of the latter (see *Ann. Perad. loc. cit.*). If not a distinct species, it must be referred to *Fomes lucidus*, being related to the latter exactly as *Fomes annularis* is to *Fomes applanatus*.

Fomes oroflavus Lloyd (Cunningham, p. 218) owes the yellow colour of the lower surface to some change in drying, whether drying after collection or drying naturally in the field. The yellow colour may occur in both *Fomes lucidus* and *Fomes applanatus* (*australis*). Several years ago I divided a large specimen of *Fomes lucidus* into three parts, and dried one in a water oven, another in the sun, the third being left to dry on the laboratory table. One of the last two turned yellow, but I regret that I cannot now lay hands on my notes and, consequently, am not sure which it was. My observations were sent to Lloyd, with parts of each specimen.

Cunningham (p. 234) refers *Polyporus dissitus* B. and Br. to *Polyporus adustus* (Willd.) Fr., and concerning the latter he states, "The smoky grey, short tubes, and effuso-reflexed pileus are the characters of the species." *Polyporus dissitus* is generally dimidiate, pure white, watery and spongy, with the hymenium subtranslucent. The hymenium turns black only in decay or when dried; it is white when fresh. *P. dissitus* is not identical with *P. adustus*.

On p. 235, Cunningham cites Ceylon as a locality for *Polyporus Braunii* Rabenhorst. As stated in *Ann. Perad.* VI, p. 107, this species was listed by Cesati from Ceylon under the name, *Polyporus rufoflavus*, the specimen having been collected by Beccari at Colombo; but as Cesati described the specimen as laccate, he probably had *Polyporus lucidus*, the lower surface of which may turn yellow in drying.

387.—*Xenostele.*

Aecidium echinaceum Berk., described from specimens on *Actinodaphne molochina* from Ceylon, was found by Sydow to be a teleutospore form, and was transferred by him to a new genus, *Xenostele*, in *Annales Mycologici*, XVIII, p. 178, *i.e.* becomes *Xenostele echinacea* (Berk.) Syd. At the same time, he transferred to the same genus, *Puccinia Litseae* (Pat.) Diet. and Henn. as *Xenostele Litseae* (Pat.) Syd.

Xenostele Litseae is common at Nuwara Eliya, Ceylon, on *Litsea fuscata* Thw., on which it causes small hemispherical galls on the leaves, or elongated pulvinate swellings, up to a foot in length, along the branches. From these galls the fungus projects

in the form of white or brownish hard cones, up to 1 mm. high and 0·5 mm. in diameter at the base, each cone being separately, and rather loosely, socketed in the gall. Hundreds of these fructifications may arise from a single stem gall.

The cone is solid, and composed of cells which resemble the pseudo-peridial cells of an aecidium. These cells are elongated, quadrangular, polygonal, or fusoid, up to 60 μ long and 20 μ broad, hyaline, with a strongly verrucose wall.

The cone does not dehisce, or open after the manner of an aecidium. When the fructification is mature, the solid cone drops out of its socket, leaving a cup (the tissue of the host plant) which contains the teleutospores. The teleutospores are comparatively few and form a rufous brown powdery mass.

The teleutospores are lozenge-shaped, one-septate, with obtuse or truncate ends, thick-walled, dark yellow-brown, deeply constricted in the middle and soon dividing into two triangular spores. The pedicel is hyaline and evanescent. The complete teleutospore measures 32–40 × 20–22 μ, and there are usually present a few thick-walled, smooth, simple spores, either globose, 20–22 μ diameter, or ellipsoid, 24 × 18 μ.

Trimen stated (*Flora of Ceylon*, III, p. 445) that *Actinodaphne* was "a genus scarcely separable from Litsea." *Xenostele Litseae* does not appear to differ from *Xenostele echinacea*, and it would seem doubtful whether they are really distinct.

388.—*Exobasidium zeylanicum* Petch.

Exobasidium zeylanicum was described in *Ann. Perad.* IV, p. 299, from specimens on *Rhododendron arboreum*. In December, 1927, it was found in abundance in Nuwara Eliya on small plants of the same species, none of which was more than two feet high. Examination of these specimens gave the following results.

The gall is spherical, up to 3 cm. diameter, and solid, not an invagination of the leaf. The internal tissue is spongy and consequently the gall shrinks considerably in drying. All the galls recently seen were white, and they were in some cases so abundant on the terminal cluster of leaves that the top of the plant was bent over, and the mass of galls resembled a cluster of small apples. The gall is attached to the under surface of the leaf.

The hymenial layer on the surface of the gall is about 40 μ thick. The basidia are cylindric, about 30 μ high and 8 μ diameter, four-spored, the sterigmata being stout, conical, 4–6 μ high. The basidiospores are cylindric or subcymbiform, straight or slightly curved, 10–16 × 3–4 μ, becoming one-septate. The secondary spores are usually clavate, sometimes cylindric, ends rounded, 8–12 × 1·5–2 μ.

Exobasidium Rhododendri Cram. (*Exobasidium Vaccinii* Wor.) also occurs on *Rhododendron arboreum* at Nuwara Eliya. It forms, on the leaves, circular shallow blisters, concave above, convex below. Its basidiospores are cylindric, curved, 10–15 × 4 μ, becoming three-septate, and the secondary spores cylindric, 5–9 × 1·5 μ.

The galls formed by these two species respectively, differ completely in their structure and mode of formation. There is, however, no very marked difference in the fungi, except in the septation of the basidiospores and the size and shape of the secondary spores.

A COMPARATIVE STUDY OF SPECIES AND STRAINS OF HELMINTHOSPORIUM ON CERTAIN INDIAN CULTIVATED CROPS.

*By M. Mitra, M.Sc., Ph.D., F.L.S.**

(With Plate IX and 13 Text-figures.)

A. Introduction.

Many species of the genus *Helminthosporium* are common parasites of various members of the Gramineae, and some of them cause diseases of considerable economic importance, such as the "stripe disease of barley," "blight of maize," "foot-rot of wheat," etc. Such diseases have been recorded from many parts of the world, more particularly from Europe, America and Japan. Similar records have from time to time been made for India, but so far no attempt has been made to carry out a systematic study of the forms occurring there and to compare them with species described in other countries. I have been engaged for some years on the study of forms of *Helminthosporium* occurring naturally on various graminaceous (and other) hosts in India.

B. Species of *Helminthosporium* already known to occur in India.

The number of species of *Helminthosporium* described by Saccardo (32) as occurring on various grasses is about thirty-five. To this list must be added a few which have been described since, more particularly by Drechsler (12) and Nisikado (25). On the other hand a number of species of Saccardo's list have been found invalid as the result of recent careful comparative study.

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The species known to occur in India up to the year 1918 are given by Butler (4) as follows:

H. Avenae Eidam, on oats.

H. gramineum Rabenh., on barley.

H. teres Sacc., on barley.

H. turcicum Pass., on maize and sorghum.

H. nodulosum Berk. and Curt., on Marwa (*Eleusine coracana* and *E. aegyptica*).

H. Sacchari Butl., on sugar-cane.

In 1922 Sundararaman reported a species of *Helminthosporium* on leaves of rice in Madras. From inoculation experiments he was able to prove the parasitic nature of the fungus, but no specific diagnosis of it was given. In 1923 I published an account of a comparative study of the forms of *H. turcicum* on maize and sorghum from which it was concluded that they were identical.

C. Indian strains and species of *Helminthosporium* studied in the present work.

The list of *Helminthosporium* forms used in the present comparative study is given below. Some forms (Nos. 1, 2, 7, 8) have proved on examination to be described species and are recorded as such. The remainder differ in greater or less degree from known forms. They will therefore be referred to for the present under a symbol notation.

1. *H. sativum* Pamm. King & Bakke, from leaves of wheat at Pusa. (*W.*)*

2. *H. sativum* Pamm. King & Bakke, from leaves of barley at Pusa. (*B.*)

3. *H.* sp. from wheat plants showing foot-rot from Poona. A species of *Rhizoctonia*, capable of producing foot-rot, was also present. (W_p.)

4. *H.* sp. from wheat plants similar to those of (3) but originating from Nagpure, Central Provinces. (W_{cp}.)

5. *H.* sp. from the leaves of *Panicum frumentaceum* at Pusa. (*P.*)

6. *H.* sp. from leaves of ginger (*Zingiber officinale*) at Pusa. (*G.*)

7. *H. Sacchari* Butl., from leaves of sugar-cane at Pusa. (*S.*)

8. *H. Oryzae* Br. de Haan, from leaves and ears of rice at Pusa. (*R.*)

The occurrence of *Helminthosporium* on *Panicum frumentaceum* and on ginger is here reported for the first time. Species of *Helminthosporium* have previously been recorded on wheat, barley and rice in India, but up to the present these have been insufficiently diagnosed.

* For simplicity these forms will be referred to in the text by these symbols.

In addition, the writer has observed the occurrence of forms of *Helminthosporium* on various wild grasses such as *Cynodon*, *Andropogon*, *Panicum* spp., *Eleusine indica*, and it is proposed to carry out comparative studies on these later.

The forms above mentioned definitely fall within the limits of the genus *Helminthosporium*. There are, in addition, certain closely related parasites on various cereals, sugar-cane and other grasses in India which on morphological grounds, such as the detailed structure of the conidiophore and conidia, are more correctly placed in the genus *Acrothecium*, although various writers, *e.g.* Drechsler (12), Palm (30), Henry (14), and others have described very similar ones as species of *Helminthosporium*. In a recent paper Mason (19) has upheld the view put forward by the writer in an earlier paper (20) that the two genera *Acrothecium* and *Helminthosporium* should be kept apart. These *Acrothecium* species will not be dealt with in the present paper.

D. Description of disease symptoms on the various host plants affected and general morphological features of the parasites as occurring naturally.

(1) *Helminthosporium sativum* Pamm. King & Bakke on wheat. (*W.*)

This fungus causes a foot-rot and root-rot of wheat to a small extent but it occurs more commonly as a leaf parasite. The disease usually appears in the early stages of growth of the wheat seedlings, forming small yellowish oval to oblong spots which increase in size (up to 2–5 × 3–10 mm.) with the growth of the host. All the vegetative parts of the plant may be attacked, and normally these only, but in severe cases spotting of the floral parts (glumes, paleae and pericarp) may be shown. The spots when mature are light brown to dark brown, oval or oblong, or irregular by the coalescence of several spots. The central region of the spot is straw-coloured to greyish brown and bears the conidiophores with the conidia. The margin of the spot is in the form of a yellowish zone which gradually merges into the normal green of the healthy leaf. The typical appearance of wheat affected by this disease is illustrated in Pl. IX, fig. 1.

The conspicuous symptoms of the rare root- and foot-rot forms of the disease are the dwarfing or arrested development and frequently the killing of the plants affected. In extreme cases the seedling is killed before it emerges from the soil. The fungal lesions are readily seen as brown rotted areas on all the underground parts.

The disease occurs in various provinces of India, but in none of these, with the exception of Burma, does it appear as yet to have caused much damage.

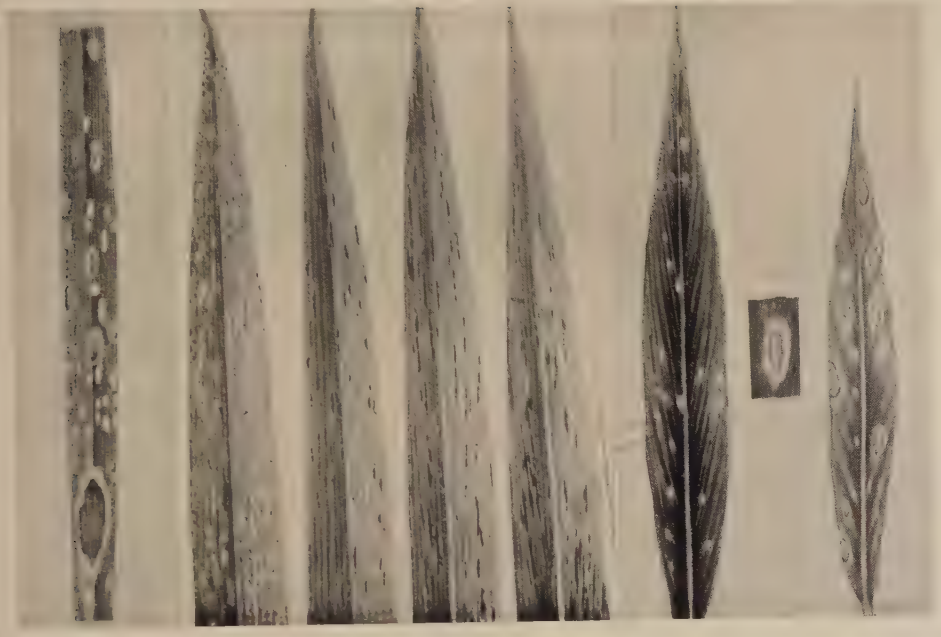


Fig. 1. Fig. 2. Fig. 3.

Fig. 4.

The conidiophores arise from the central dead portion of the spot, either emerging through stomata or directly piercing the cuticle. They occur singly or in fascicles of two to four and occasionally of five. The conidiophore bears a single terminal spore, then proceeds to send out a branch just behind the apex. This branch repeats the process, and so on, until a series of about five or six spores is formed. It is thus a cymosely branched structure with a series of geniculations, each bend of the conidiophore corresponding to the point of attachment of a spore. When the latter has fallen, a permanent scar remains on the conidiophore.

The conidiophores are septate, slightly swollen at the base, and dark olivaceous brown with sub-hyaline tips. The normal dimensions are 120–205 × 7–8·5 μ, though occasionally conidiophores reaching 350 μ in length have been observed.

The spores are 26–125 × 11·5–22·5 μ, straight or slightly curved, 3–11 septate as a rule with tapered sides and rounded ends. The colour is brown to dark brown olivaceous, all the cells being concolorous. The outer spore wall is thick and conspicuous and there is a distinct hilum at the basal end. Irregularly shaped, *e.g.* bilobed or twisted spores, and spores of very low septation (0–1) are occasionally seen. Germination takes place from the polar cells only, except when the latter are injured. In bilobed spores germination takes place from each end cell.

Numerous isolations were made from wheat plants showing the above symptoms and growing in the Pusa district. The same organism was obtained always. Isolations from diseased material derived from Burma gave a strain somewhat different from the typical Pusa strain but closely resembling both in its morphological and parasitic characters the type of *Helminthosporium* occurring on barley in the Pusa district.

The two strains derived from wheat readily produced attack with all the characteristic symptoms when inoculated on wheat plants. Monospore cultures of the two strains were used in these tests.

It may be stated here that similar inoculation experiments were made with all the strains dealt with in this paper, with similar results in each case.

(2) *Helminthosporium sativum* Pamm. King & Bakke on barley. (*B.*)

The general symptoms of this disease are very much as have been described in wheat. The attack on barley under Indian conditions is however generally of a more severe type. Thus the foot- and root-rot phases of the disease are more commonly met with, with resultant partial failure, stunting, etc., of the crop.

The leaf spots, which are of a darker brown than in wheat and which do not show the characteristic yellow ring, tend to coalesce into long stripes running up and down the leaves (though not to the extent shown by another species, *H. gramineum* Rabenh.). Often also there is considerable spotting of the glumes and pericarp. From observations carried out in the neighbourhood of Pusa it is clear that the disease is more severe where barley has been cultivated continuously on the same plot of land, and there is strong evidence that a considerable amount of infection from the soil takes place.

The morphological features of this parasite as seen on the host plant are practically identical with those of the wheat strain described above.

(3) and (4). Strains W_p and W_{cp} on wheat.

These organisms were isolated from material derived from Poona and the Central Provinces respectively. The only symptoms shown were foot-rot; that is, on the material available, which was limited in quantity, there were no leaf spots and therefore no naturally occurring conidia. Isolations were made from the internal tissue of the stem bases (after the usual treatment with mercuric chloride) and two organisms were obtained, differing in their cultural features from the typical strain on wheat. By artificial inoculations it was shown that both new forms were capable of causing leaf spotting in addition to foot-rot.

(5) Strain *P* on *Panicum frumentaceum*.

This fungus is found every year in the neighbourhood of Pusa and causes considerable damage to the plants affected. The first symptoms of the disease are seen during the rainy period (July–Sept.) in the form of very numerous small (1–2 mm. diameter) yellowish dot-like discolorations on both sides of the leaves and on the leaf sheaths. These spots gradually increase in size and show a light brownish centre surrounded by a yellowish margin. They extend longitudinally parallel to the veins and often cross the latter. By the coalescence of several such spots long stripes are formed. The older spots are dark brown or chocolate-coloured in the centre, and there is abundant formation of conidiophores and conidia in these parts. The typical appearance of the disease on leaves is illustrated in Pl. IX, fig. 2.

The conidiophores, which differ only slightly from those of *H. sativum* described above, range in length from 62 to 263 μ and in diameter from 4·5 to 7 μ. The conidia are however distinct, being fusoid, straight or rarely slightly curved, 3–11 septate with slight constrictions at the septa. They vary in colour from

yellowish when young to light yellowish brown when mature. They are pointed at the basal end with a distinct hilum and measure 75–125 × 11·5–18·5 μ.

(6) Strain *G* on ginger.

This fungus, like the preceding, occurs frequently in the neighbourhood of Pusa. The first symptoms of the disease appear during the rainy months in the form of small oval discolorations (4–5 × 2–3 mm.) scattered over both surfaces of the leaves. After the rains these spots develop rapidly, increasing in size and showing a brownish centre and yellowish margin which gradually merges into the normal leaf. The mature spot consists of a central dead straw-coloured area surrounded by a brown ring outside which is the yellowish zone (*v.* Pl. IX, fig. 3).

The conidiophores which arise from the central dead area of the spot are of the type already described. The conidia are brown, 3–9 septate, straight to more frequently crescent-shaped, round at both ends, 43 to 109 μ in length and 11·5 to 20 μ in width.

(7) *H. Sacchari* Butl. on sugar-cane. (*S.*)

This fungus, which was named in 1913, is in all probability identical with *Cercospora Sacchari* described from Java by Breda de Haan in 1892 and later from the same country by Wakker and Went (38), Krüger (18), and Dickhoff and Hein (10). Under the latter name it was also described by Cobb in 1909 as the most destructive leaf disease of sugar-cane in Hawaii. In 1918, *i.e.* subsequent to the date of publication of Butler and Hafiz's paper, Van der Bijl and Paul described as *Cercospora Sacchari* a fungus occurring on sugar-cane in South Africa, but expressed the opinion that the fungus is more like a *Helminthosporium*. From a study of the illustrations given by various writers, especially Cobb (8) and Wakker and Went (38), it appears very probable that the two fungi are the same and that Butler and Hafiz's attribution is the correct one.

The parasite has also been reported from the Philippines by Johnston (16), from the West Indies by Johnston and Stevenson (17), and by Cook (9) from Porto Rico. One may say therefore that it appears to be present in most countries where sugar-cane is grown.

Under Indian conditions it has not been found to cause appreciable damage, and as far as I am aware has been reported only from Bihar. The disease, which is known as "eye-spot," appears at any time throughout the year though more frequently after the monsoon.

According to Cobb the disease spots are chiefly on the upper

surface of the leaves, but in the material from Pusa they are equally distributed on both sides.

The morphology of the fungus as shown on the host agrees with that described for *H. sativum* with the two following points of difference. In the invaded region certain epidermal cells become filled with interwoven mycelium forming stromatic masses, and creeping brown hyphae are formed on the surface. In both these respects the sugar-cane fungus agrees with the one next to be described and differs from all the preceding.

The conidiophores (70–200 × 5·5–7·5 μ), which are of a deep greenish brown with paler tips, arise from the stromatic masses or from the creeping hyphae already mentioned. Occasionally they may reach a length of 300 μ. They have never been observed to emerge from the stomata after the manner of *H. sativum*. The conidia are light olive-green to greenish brown, cylindrical, oblong or elliptical and often slightly curved with rounded ends, 3–10 septate. The spore size as given by Butler and Hafiz is 35–60 × 8·5–12 μ. A study of more extensive material, especially at different times of the year, shows that the above figures do not indicate the full range of variability, which is 32–120 × 11–17 μ. These measurements agree very closely with those given by various workers on "eye-spot" disease.

Text-fig. 1. Floral parts of rice plant affected by *H. Oryzae*.

(8) *H. Oryzae* Br. de Haan, on rice. (*R.*)

This species was first reported from Java as a parasite on rice by Breda de Haan (2), though previously a similar fungus had been described as a saprophyte by Thümen (35). Hori (15) recorded it from Japan shortly afterwards. More recent work which is summarised by Drechsler (12) and also by Nisikado and Miyake (26) has shown that the fungus is present in all important rice-producing countries. According to Drechsler and Ocfemia (29), all the organisms described in this connection are identical. On the other hand Nisikado (24) in a recent paper considers that the American strain is different from the Japanese and may possibly be a different species.

H. Oryzae is a very common parasite of rice in India producing the disease known as "sesame leaf-spot" and has been reported from almost all the rice-growing provinces. Its occurrence in

India was first reported without specific determination by Sundararaman (34) from Madras, but it is clear from a study of his drawings and from herbarium material that the fungus concerned was *H. Oryzae*.

Under Indian conditions the disease occurs both as a leaf-spot and as a seedling blight. The lesions are formed not only on leaves and leaf-sheaths but also on the floral parts, glumes and pericarp, as illustrated in Text-fig. 1. Heavily infected grains are shrunken and either fail to germinate or produce diseased seedlings which die at an early stage of development. The leaf-spots, which are at first pale brown and later brown, occur in large numbers on both sides of the leaves.

The conidiophores arise either through the stomata or from stromatic masses present in the epidermal cells, when penetrating directly through the cuticle. They are also formed directly from the vegetative mycelium on the surface of the dead central area of the spot. The last method is very commonly found on infected glumes. The conidiophores may be very long, up to 350 μ (according to Nisikado and Miyake, 550 μ), and creep over the surface. The basal swelling is particularly marked. The conidia are elliptical, fusiform, slightly bent to one side, yellowish brown to deep olive brown, 5–11 septate, thick walled with blunt end cells and measure 50–133 × 15–22·5 μ.

E. Study of various forms under conditions of artificial culture.

The eight species or strains listed in Section C, some of which were isolated in India and others in England from material obtained from India, were subjected to a lengthy series of cultural experiments with a view to a better understanding of their physiological features and their variability under different environmental conditions. Some of these forms had already been purified by the method of single spore culture. At the beginning of this work the purity of all the forms was further assured by carrying on each form from a single hyphal tip (3).

The fungi were cultivated both in tubes and on plates. The following were the media chiefly used:

Synthetic: Brown's agar; Brown's starch agar; Richard's solution agar.

Natural: prune juice agar (20 gm. of unstoned prunes to one litre of water); oatmeal agar (33 gm. of oatmeal to one litre of water); sterilised straw in test tubes (wheat, oats, barley and couch grass).

Other media occasionally used were apple extract agar, potato extract agar, Dox's agar, and sterilised rice in tubes.

(1) *Linear growth-rate under different environmental conditions.*

The influence of temperature upon growth-rate is of greatest importance. Subsidiary factors are the depth of the cultural medium and the presence or absence of light during growth.

Depth of cultural medium. The effect of different depths of cultural medium is illustrated in Table I which represents the growth of all the eight forms on Brown's agar. The Petri dishes used were all of the same diameter, so that the depths of medium are proportional to the quantities given in the table.

Table I. *Linear growth (mm.) of eight forms of* Helmintho-sporium *on Brown's agar after* 10 *days at* 20° *C.*

Fungus	Plates with 60 c.c. of medium	Plates with 30 c.c. of medium	Plates with 15 c.c. of medium
W	88·5	60·3	39·2
B	82·3	65·0	29·7
W_p	90·0	59·5	35·0
W_{cp}	40·0	42·3	70·8
P	110·0	105·0	99·8
G	41·0	41·0	35·5
S	86·0	65·0	56·0
R	107·7	97·3	65·0

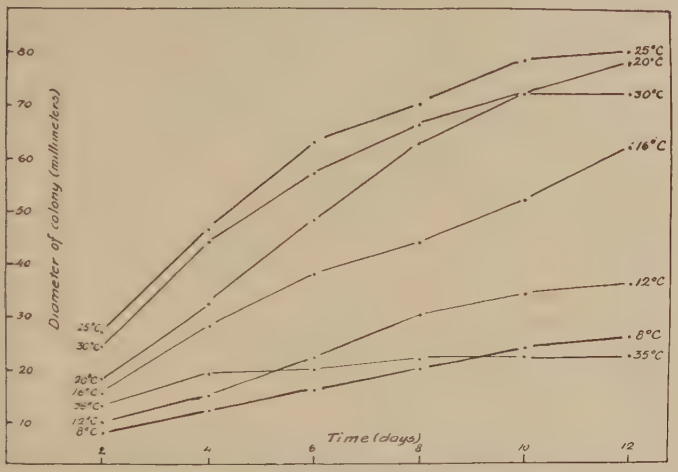
From the table it is clear that the amount of growth as measured by linear expansion in general increases with the depth of medium within the limits of the experiment. A definite exception is seen in the strain W_{cp}, where the converse relationship holds. This result was confirmed in a series of tests with slant cultures in plates when it was observed that the greater radial expansion in general took place in the direction of the shallow side.

From these results it is clear that, in carrying out determinations of growth-rate under different environmental conditions, it is essential that care should be taken to ensure uniformity of depth in the different plate cultures.

Light. The effect of exclusion of light is in general to reduce the rate of linear growth as is shown in Table II. This experiment was carried out with plates of Brown's agar at laboratory temperature, one set being exposed to the alternation of day and night, and the other being kept darkened throughout, though otherwise under the same conditions. The retarding action becomes more pronounced as time goes on, as is seen by comparison of the figures in the third and fifth columns of Table II.

Temperature. The rates of growth of the various forms at different temperatures were studied on the three synthetic media and on prune juice agar. The plates used were of uniform diameter and into each was poured 50 c.c. of medium so that the

depth was uniform. These experiments were usually run in triplicate.



Text-fig. 2. Temperature relationships of *H. sativum* (wheat strain) on Brown's agar.

Table II. *The effect of light and darkness on growth on Brown's agar of eight forms of* Helminthosporium.

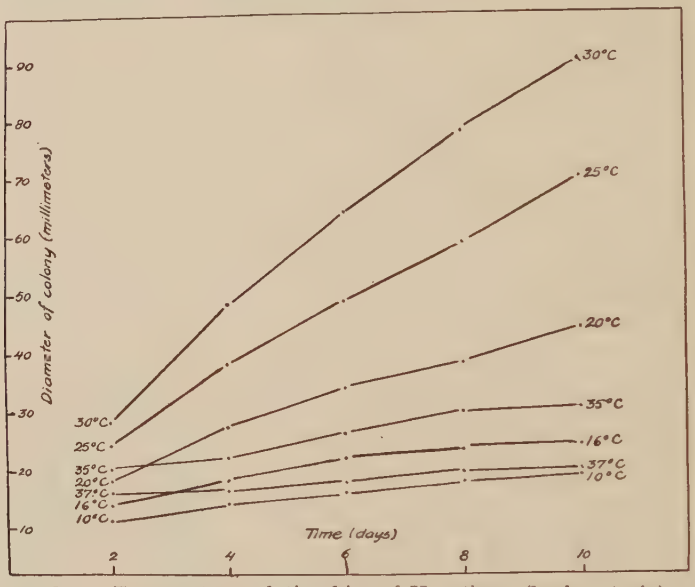
Fungus		5 days' growth	Ratio D./L.	11 days' growth	Ratio D./L.
W	L.	33·9	89·0	81·0	83·0
	D.	30·1		67·3	
B	L.	37·1	99·7	78·5	91·3
	D.	37·0		71·7	
W_p	L.	36·5	95·8	84·7	87·6
	D.	35·0		74·2	
W_{cp}	L.	26·7	77·5	39·2	67·7
	D.	20·7		26·5	
P	L.	32·2	93·7	88·0	87·1
	D.	30·2		76·7	
G	L.	15·2	126·3	29·0	113·4
	D.	19·2		32·9	
S	L.	27·5	106·6	60·3	88·7
	D.	29·6		53·5	
R	L.	42·5	88·2	93·0	87·3
	D.	37·5		81·2	

(L., in the light. D., in the dark.)

The general relation between temperature and linear growth is shown in Text-fig. 2, which gives the rate of spread of *H. sativum* (wheat) on Brown's agar over a series of temperatures.

From Text-fig. 2 it is seen that at lower temperatures the

rate of growth continues more or less uniformly, but that at higher temperatures the initial rate of growth is not maintained, as is clear by the bending over of the curves (*e.g.* the curve for 30° C.). The diameters of the colonies at the lower temperatures thus tend to overtake those at the higher, or in other words the optimum temperature for rate of linear growth becomes lower as time goes on. This is a feature common to fungi which show a tendency to the staling type of growth.



Text-fig. 3. Temperature relationships of *H. sativum* (barley strain) on Richards' solution agar.

Similar series of curves have been constructed for all the other forms on all the four media. As is to be expected, the various curves so obtained show a general resemblance with certain differences in detail. The main points brought out by comparison are as follows:

The tendency noted above for staling effects to appear at the higher temperatures varies somewhat from one medium to another with the same fungus. Thus it is less marked on Brown's starch agar, which has a higher carbon and lower nitrogen content than the standard medium, with the result that the optimum temperature for growth is higher throughout. Richards' solution agar and prune juice agar give in general higher optima for growth than Brown's medium. This is illustrated in Text-fig. 3, which represents the growth on Richards' solution agar of

H. sativum from barley, over a range of temperatures. Here it will be observed that the growth at 30° C. is distinctly greater than at 25° C. in contrast to the result shown in Text-fig. 2.

The approximate optima for linear growth of all the forms on the four media used are given in Table III below:

Table III. *Optimum temperatures* (° C.) *for various forms of* Helminthosporium *on different media.*

Fungus	Brown's agar	Brown's starch agar	Richards' solution agar	Prune juice agar
W	25	25	30	30
B	25	25–30	30	30
W_p	25	25–30	30	25–30
W_{cp}	25–30	30–35	30	30–35
P	25	30	30	30
G	25–30	25	25–30	30
S	30	30	30	30
R	25	30	30	30

Text-fig. 4 illustrates the growth of all the strains on Brown's agar at temperatures in the neighbourhood of the optimum. The curves represent the diameters for each strain after eight days' growth. It should be noted in particular that of the three forms isolated from wheat, two have optima in the neighbourhood of 25° C. and the third (W_{cp}) near 30° C. On this medium the majority of the strains have optima round 25° C. On the other hand, as shown in Table III, all the strains show higher optima when grown on the other three media.

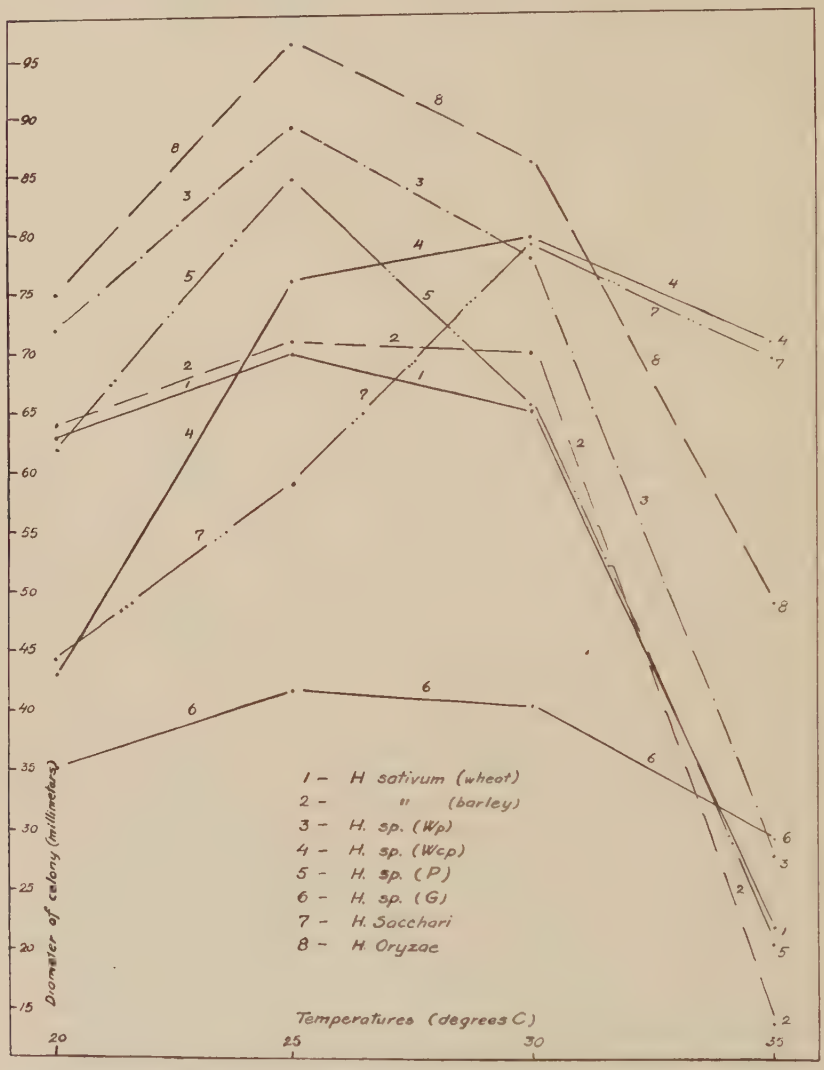
A striking feature shown in Text-fig. 4 is the slow rate of growth of the strain from ginger (*G*). This is equally well marked on all the other media. From this point of view therefore the strain from ginger is sharply demarcated from the remainder. The same kind of slow growth is shown by one of the strains derived from wheat, viz. strain W_p, but only on Richards' solution agar and prune juice agar.

The minimum temperature for each strain was found to be below 7° C. but it was not accurately determined. At 37° C. all the forms showed slow growth, but none at 40° C. with the exception of *H. Sacchari* and *H. Oryzae*. The fact that the spores of *H. Oryzae* are able to germinate at 41° C. is also noted by Nisikado and Miyake (26).

The thermal death points* of all the strains were determined and found with one exception to be between 63–64° C. Spores of the strain from *Panicum frumentaceum* were more sensitive to heat, being killed at 61° C. It is perhaps interesting to note that

* In these determinations the spores were enclosed in a fine glass capillary, rapidly heated, and maintained at the given temperature for five seconds.

this is the only one of the species tested which possesses lighter coloured spores. In both respects therefore this strain appears



Text-fig. 4. Eight days' growth of different forms of *Helminthosporium* at various temperatures on Brown's agar.

to approximate to a typical member of the series to which *H. gramineum* belongs.

From the above account it is clear that all the eight forms show somewhat different quantitative reactions as regards the effects of temperature. The more distinctive results emerging from this comparison may be summed up as follows:

(1) The high optima shown by strain W_{cp} and by *H. Sacchari*.

(2) The high maxima shown by *H. Sacchari* and *H. Oryzae*.

(3) The slow rate of growth of strain *G*.

(4) The greater sensitiveness to heating of the spores of strain *P*.

(2) *Variation of macroscopic growth features under different environmental conditions.*

Aerial mycelium. The degree of development of aerial mycelium varies with each strain according to the environmental conditions and with the different strains under the same conditions. In all strains increase of temperature leads to increased formation of aerial mycelium up to the neighbourhood of the optimum for superficial growth. Above the latter temperature the type of growth tends to became hard or felt-like, with progressive reduction of the loose aerial mycelium the higher the temperature.

Many of the strains, especially when grown on certain media, show in culture localised mycelial areas differing in appearance from the surrounding parts. These "patches" appear more commonly at higher temperatures and in older cultures and represent saltant areas.

Other conditions being the same, the amount of aerial mycelium is greater in cultures exposed to alternating day and night than in those kept in total darkness. Similarly high atmospheric humidity favours strong development of aerial mycelium, and conversely.

The nature of the culture medium very markedly affects the amount of aerial mycelium. All the strains have been tested in this respect, with the following general results:

(1) Rich media such as Richards' solution agar give more profuse development of aerial mycelium than poorer media such as Brown's agar.

(2) Progressive reduction is seen in successive dilutions of the same medium.

(3) With the same concentration of the same medium the amount of aerial mycelium becomes less, the shallower the layer of medium used.

In spite of the variability indicated above, it is nevertheless true that each strain is more or less characterised by the amount of aerial mycelium which it forms. Thus when the strains of *H. sativum* from wheat and barley are compared under similar

conditions the former always shows the greater development of aerial mycelium. Other strains with tendency similar to the strain of *H. sativum* from wheat are W_{cp}, *P*, *H. Oryzae* and *H. Sacchari*. The strain W_p shows intermediate characters with a tendency to form a crust-like type of mycelium, especially on Richards' solution agar, though on the same medium when diluted 50 to 100 times it forms a uniform almost creeping and spreading mycelium. The strain *G* forms practically no aerial mycelium on any of the media tried.

A certain amount of difference also arises between the various forms with regard to the lobed or unlobed nature of the growing margins. This again is a feature that may be modified to some extent by cultural conditions. Thus the strains of *H. sativum* from wheat and barley have a lobed appearance on prune juice agar but not on the other three media tested. *H. Sacchari* shows the same appearance on Brown's starch agar as well as on prune juice agar. The strains W_{cp}, *P*, and *G* and *H. Oryzae* grow in the unlobed manner on all the media.

Colour. The colour of the different strains is fairly constant, varying through different shades of grey according to the media employed. The amount of variation shown on different media is indicated in Table IV.

The effect of temperature on colour is slight apart from a tendency to reduction of the latter at temperatures above the optimum.

Table IV. *Colour of various forms of* Helminthosporium *on four media.*

	Colour of colony on various media			
Fungus	Brown's agar	Brown's starch agar	Richards' solution agar	Prune juice agar
W	White to pale gull grey	Pale gull grey	Dark gull grey	Gull grey
B	Deep neutral grey	Deep neutral grey	Deep neutral grey	Deep neutral grey
W_p	Dark olive grey	Dark green grey	Dark bluish grey green or mouldy	Dark bluish grey green
W_{cp}	Drab grey	Drab grey	Drab grey	Pallid purplish grey
P	Olive grey	Pale neutral grey	Light vinaceous grey	Pale neutral grey
G	Dark greenish brown	Dark greenish brown	Dark greenish brown	Dark greenish brown
S	Brownish drab	Dark olive grey	Dark olive grey	Castor grey
R	Pallid purple drab	Dark olive grey	Pale smoky grey	Dark greyish olive

Light. Light is a factor of some importance in colour formation. Cultures grown in the absence of light are darker, while those which have been exposed to alternating day and night show a characteristic pinkish tinge.

Zonation. The chief determining factor of zonation is the alternation of light and darkness. It was pointed out above that the amount of development of aerial mycelium was influenced by light, so that the necessary condition is forthcoming for the formation of daily zones. An exception occurs in strain *G*, which does not form aerial mycelium under any of the conditions tried, neither, in consequence, does it show any zoning. More or less distinct zoning is seen in cultures of the other seven strains. This effect is always most clearly marked in the neighbourhood of the optimum temperature. The influence of the nature of the medium is illustrated in Table V.

Table V. *Zonation on different media at optimum temperature in eight forms of* Helminthosporium.

Fungus	Brown's agar	Brown's starch agar	Richards' solution agar	Prune juice agar
W	× ×	×	—	×
B	×	—	—	×
W_p	—	× ×	—	—
W_{cp}	×	× × ×	× ×	—
P	×	×	—	—
G	—	—	—	—
S	×	—	—	×
R	—	—	—	—

(— = no zonation, × = slight, × × = moderate, × × × = good zonation.)

As shown in the above table, strain W_{cp} gives the most distinctive zoning effects. It may be noticed also that this is the only strain which shows zonation when grown on Richards' solution agar.

The systematic study of growth-form in relation to environmental factors was carried out on the three synthetic media and on prune juice agar. Numerous cultures were also made from time to time on a large variety of other media. The following is a résumé of the main cultural features observed.

On plain agar (1·5 per cent.) all the strains show good growth in area, but there is practically never any aerial mycelium and sporulation is poor.

On potato extract agar, wheat broth agar, corn meal agar, oatmeal agar, apple extract agar, glucose peptone agar, and Dox's solution agar, all the strains, with the exception of that from ginger, show good development of aerial mycelium. On all these media the type of growth, though differing in various

details, shows a general resemblance to that on Brown's starch agar.

In tubes of sterilised straw (wheat, oats, barley and couch grass) there is very poor development of aerial mycelium though a good deal may appear on the liquid extract at the bottom of the tube. These media are especially useful for spore production, the surface of the straw being covered with a thin creeping mycelium which bears a heavy crop of spores.

The four strains originating from wheat and barley were cultured on tubes of boiled rice. On this medium there is abundant mycelial growth. The individual swollen rice grains become penetrated with hyphae and finally as hard mycelial sclerotium-like bodies of a bluish to greenish grey colour. The aerial mycelium also tends to aggregate into compact masses somewhat resembling sclerotia, as illustrated in Pl. IX, fig. 4.

(3) *Variation of microscopic growth features under different environmental conditions.*

The amount of sporulation is to a certain extent a macroscopic character, but in *Helminthosporium* species it cannot be determined with certainty without microscopic examination. For this reason it will be dealt with in this section.

The optimum temperature for sporulation in all strains is in the neighbourhood of 25° C. No spores are formed below 10° C., except in the strongly sporing form from ginger, which gives slight sporulation even at 7° C. At 35° C. all the strains are sterile, except *H. Sacchari* which shows slight sporulation.

Exclusion of light sometimes increases sporulation. This is especially well marked with *H. Sacchari* and with the strain W_p. In other cases, *e.g. H. sativum* from barley, and *H. Oryzae*, the effect, if it occurs at all, is negligible.

Conditions of high humidity somewhat favour sporulation. Thus when plates are grown upside down over a water surface, there is more sporulation than in plates similarly held over a 10 per cent. solution of sulphuric acid (humidity about 87 per cent.).

A striking response in the form of local sporulation is often seen as the result of wounding. Thus in a poorly sporing culture a good development of spores can be produced by scoring the surface of the medium with a sterile knife. After a few days fairly strong sporulation has taken place along the line of and a short distance away from the cuts. The same effect is even more marked if a piece of the non-sporing culture is cut out and incubated in a saturated atmosphere in a fresh sterile dish.

Other factors being the same, the amount of sporulation shown varies in different media and with different strains. A general

summary of the behaviour of all the eight forms on six media is given below in Table VI.

Table VI. *Sporulation of eight forms of* Helminthosporium *on six media.*

Fungus	Brown's agar	Brown's starch agar	Richards' solution agar	Prune juice agar	Oatmeal agar	Straw
W	×	× ×	× ×	× ×	× ×	× × ×
B	× ×	× × ×	× × ×	× × ×	× × ×	× × × ×
W_p	×	× ×	×*	× ×	× ×	× × ×
W_{cp}	–	–	–	× ×	× ×	× × ×
P†	–	× ×	– –	–	–	×
G	× × ×	× × × ×	× × ×	× × × ×	× × × ×	× × × ×
S	×	× × ×	× ×	× × ×	× × ×	× × × ×
R	–	×	–	–	×	× ×

* × × on Richards' solution agar diluted 50 or 100 times.
† × × on Dox's solution agar; × on glucose peptone agar.
(– = no sporulation, × = slight, × × = moderate, × × × = good, × × × × = very good.)

Size and degree of septation of spores. With any one strain and on a given medium the only environmental factor which distinctly affects the microscopic measurements of the spores is temperature. At temperatures distinctly above the optimum, the spores produced are shorter, narrower and of lower septation. This effect is illustrated in Table VII, which gives the range of spore length, width and septation for *H. Sacchari*. Similar results were also found in the other seven strains. With these there was no sporulation at 35° C. but the spores formed at 30° C. were much shorter, narrower and less septate than those at 20° C.

Table VII. *Variation in size and septation of spores of* H. Sacchari *at different temperatures.*

Medium	Temperature (° C.)	Range of length (μ)	Range of width (μ)	Range of septation
Brown's agar	20	33–89·0	11·5–16·5	3–8
	30	30–72·5	11·5–16·5	2–7
	35	26·5–65·0	10–11·5	0–2
Brown's starch agar	20	35–82·5	13–18·5	3–9
	30	20–72·5	11·5–16·5	0–8
	35	20–49·5	11·5–13·0	0–5
Prune juice agar	20	30–82·5	11·5–18·5	3–9
	30	30–79·0	11·5–15·0	3–9
	35	30–62·5	8–13·0	0–6
Richards' solution agar	20	23–82·5	11·5–18·5	3–8
	30	21·5–75·0	10–15·0	0–8

Sometimes, more particularly with *H. sativum* and strain W_p, it was also seen that reduction in size and degree of septation took place when the fungus developed at a low temperature (10–12° C.).

The variation of spore length and width in the different forms on different media at a uniform temperature of 20° C. is given in Table VIII. The figures in the table are each based on a count of 100 spores. The measurements were made in such a way as to eliminate unconscious selection of spores.

Table VIII. *Variation in length and width of spores of various forms of* Helminthosporium *on different media at 20° C.*

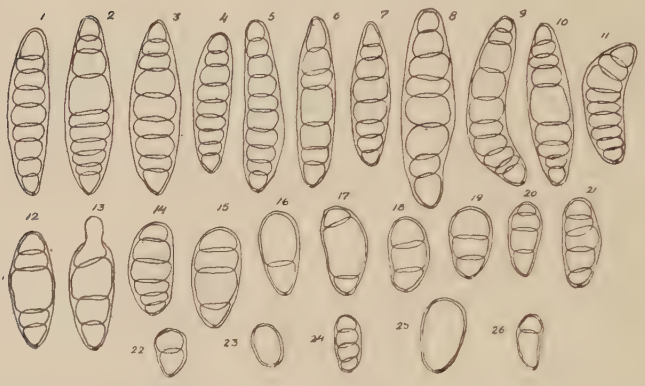
Fungus	Medium	Range of length (μ)	Average length (μ)	Range of width (μ)	Average width (μ)
W	Oat straw	40–93	81·1	17–27	21·7
	Oatmeal agar	20–102	77·0	17–27	22·4
	Prune juice agar	20–79	51·7	13–23	18·7
	Brown's agar	33–86	67·2	17–27	21·0
	Richards' solution agar (normal)	20–56	39·5	13–23	18·0
	Richards' solution agar (*N*/100)	30–96	73·3	13–27	20·6
B	Oat straw	33–86	81·2	17–23	21·0
	Oatmeal agar	49–96	71·6	17–27	22·3
	Prune juice agar	17–86	59·4	13–27	19·9
	Brown's agar	49–96	71·3	17–27	22·0
	Richards' solution agar (normal)	23–86	65·7	13–23	18·9
	Richards' solution agar (*N*/100)	27–93	77·6	15–23	21·2
W_p	Oat straw	23–73	47·2	10–19	14·2
	Oatmeal agar	17–79	55·8	12–20	15·2
	Prune juice agar	23–69	47·7	10–17	13·3
W_p	Richards' solution agar (*N*/100)	27–69	53·8	10–19	13·5
W_{cp}	Oat straw	27–66	52·3	13–20	16·6
	Oatmeal agar	23–69	52·5	13–20	16·0
	Prune juice agar	30–73	51·7	13–20	16·9
P	Oat straw	49–145	98·4	10–17	12·6
	Brown's starch agar	63–126	103·5	12–19	14·4
	Dox's agar	69–159	124·3	12–19	15·4
G	Oat straw	36–92	69·0	13–19	15·1
	Oatmeal agar	30–109	79·4	13–19	15·6
	Prune juice agar	33–99	68·5	13–19	15·3
	Brown's agar	49–93	72·8	12–19	15·0
	Brown's starch agar	36–116	76·4	13–20	16·9
S	Oat straw	33–96	66·3	13–19	15·2
	Oatmeal agar	30–99	70·5	13–17	15·1
	Prune juice agar	30–83	61·9	12–19	15·1
	Brown's agar	39–89	62·2	12–17	14·5
	Brown's starch agar	36–83	60·2	13–19	15·0
S	Richards' solution agar (normal)	30–83	55·0	12–19	14·0
	Richards' solution agar (*N*/100)	33–103	74·5	12–19	16·5
R	Oat straw	49–122	95·3	13–22	18·5
	Oatmeal agar	49–116	90·3	13–22	18·2
	Prune juice agar	56–113	93·3	15–20	17·3
	Brown's starch agar	43–122	79·8	13–20	17·0

The main feature brought out by the above table is that prune juice agar and more especially Richards' solution agar of full strength give rise to abnormally small spores. This is shown

clearly for the two strains of *H. sativum* from wheat and barley and for *H. Sacchari*, and is illustrated in Text-figs. 5, 6 and 7. The effect is not shown in strains W_p and W_{cp}, but it will be observed that with both these the spores are small on all media. If one excludes these two media there is general agreement in spore size on the different media. Thus the spores of strains W_p and W_{cp} range round 50 μ on all media; those of both strains of *H. sativum* are of intermediate length (67–80 μ); those of the strain from *Panicum* range from 100–125 μ; and so on.

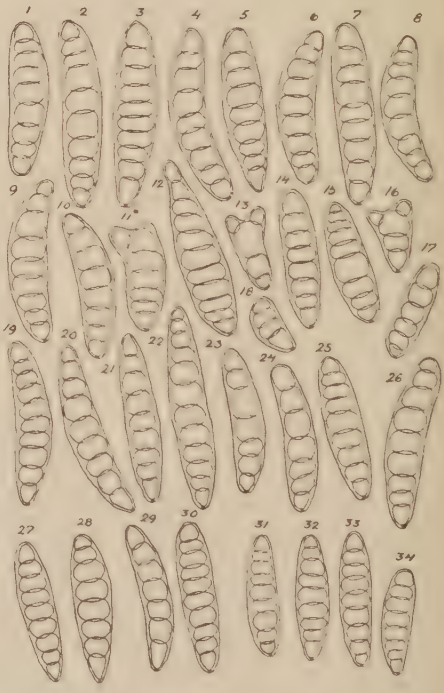
Table IX. *Variation in septation of various forms of* Helminthosporium *on different media.*

Fungus	Medium	Range of spore septation	Mode	Average
W	Oat straw	3–10	8	7·23
	Oatmeal agar	0–10	7	5·89
	Prune juice agar	0–7	7	3·86
	Brown's agar	3–8	6 & 7	5·23
	Richards' solution agar (normal)	0–6	0 & 2	2·03
	Richards' solution agar (*N*/100)	2–9	6 & 7	6·80
B	Oat straw	3–9	6	6·37
	Oatmeal agar	0–9	6 & 7	5·78
	Prune juice agar	0–9	6 & 7	4·62
	Brown's agar	4–8	6 6	6·37
	Richards' solution agar (normal)	0–9	6 6	4·50
	Richards' solution agar (*N*/100)	2–10	8 8	7·69
W_p	Oat straw	3–7	6 6	4·49
	Oatmeal agar	1–9	5 & 6	5·55
	Prune juice agar	2–8	5	5·09
	Richards' solution agar (*N*/100)	2–8	5 & 6	5·30
W_{cp}	Oat straw	2–8	5	5·59
	Oatmeal agar	2–9	5	6·32
	Prune juice agar	3–9	6 & 7	6·22
P	Oat straw	4–8	7	6·40
	Brown's starch agar	3–10	7	6·24
	Dox's solution agar	3–11	7	7·04
G	Oat straw	3–9	6	6·08
	Oatmeal agar	1–10	6	6·48
	Prune juice agar	2–10	6	6·24
	Brown's agar	3–9	6	5·60
	Brown's starch agar	2–11	6	6·04
S	Oat straw	4–9	7	6·95
	Oatmeal agar	3–10	8	8·25
	Prune juice agar	3–9	8	6·83
	Brown's agar	3–8	6	5·20
	Brown's starch agar	3–9	6	6·62
	Richards' solution agar (normal)	3–8	5	6·04
	Richards' solution agar (*N*/100)	3–11	8	7·33
R	Oat straw	4–10	7 & 8	7·43
	Oatmeal agar	3–10	8	6·67
	Prune juice agar	4–10	8	7·37
	Brown's starch agar	3–9	6	6·23



Text-fig. 5. *H. sativum* (wheat). 1–11. Spores on Richards' solution agar (*N*/100). 12–26. Spores on Richards' solution agar (*N*). (Note the smaller size and lower septation of the latter.)

Text-fig. 6. *H. sativum* (barley). 1–6. Richards' solution agar (*N*/100). 7–15. Richards' solution agar (*N*). 16–25. Oat straw.



Text-fig. 7. *H. Sacchari*. 1–12. Richards' solution agar (*N*/100). 13–18. Richards' solution agar (*N*). 19–26. Oat straw. 27–30. Oatmeal agar. 31–34. Prune juice agar.

The range of spore septation, the septation mode, and the average number of septa per spore (all being based on counts of 100 spores) are given in Table IX for the different forms of *Helminthosporium* on a variety of media.

Again it will be seen that, at least in the two *H. sativum* strains from wheat and barley, an abnormally low degree of septation is shown on prune juice agar and Richards' solution agar, as illustrated in Text-figs. 5, 6 and 7. Leaving aside these two media, there is a certain amount of irregular variation from strain to strain and from medium to medium, but it is clear that the average septation is less characteristic of the different strains than are the measurements of spore length and width.

If one excludes prune juice and Richards' solution agars, which give abnormal spores both as regards size and septation, one may justifiably take the average of the measurements given on the other media. In this way the main results of Tables VIII and IX may be condensed as in Table X.

Table X. *The average length, width and septation of spores of various forms of* Helminthosporium *on different media.*

Fungus	Average length (μ)	Average length on oat straw (μ)	Average width (μ)	Average width on oat straw (μ)	Average septation	Average septation on oat straw
W	74·6	81·1	21·4	21·6	6·3	7·2
B	75·4	81·2	21·6	20·9	6·5	6·3
W_p	51·1	47·2	14·0	14·1	5·1	4·5
W_{cp}	52·1	52·3	16·5	16·6	6·0	5·6
P	108·7	98·4	14·1	12·6	6·5	6·4
G	76·9	69·0	15·6	15·1	6·0	6·0
S	68·3	66·3	15·3	15·2	6·9	6·9
R	89·6	95·3	17·9	18·4	6·9	7·4

The figures in columns 2, 4 and 6 give the measurements as derived from a number of media, those in columns 3, 5 and 7 are the corresponding measurements taken from cultures on oat straw. It will be observed that the two sets of figures are in fairly good agreement. Hence as the oat straw medium is a very suitable one for sporulation, it does not appear that any advantage is obtained by resorting to a large variety of media if the object is simply to obtain reliable measurements of spore size and septation.

The general *spore colour* varies only slightly on different media. There is, however, a distinct variation from strain to strain. If the strains are arranged in order of increasing darkness of spores, the following series is obtained: strain *P*, strain W_{cp}, *H. sativum* from wheat, *H. sativum* from barley, strain W_p. Strain *G* and *H. Oryzae* are indistinguishable in colour from strain W_{cp}; *H. Sacchari* is similar to *H. sativum* on wheat.

The polar cells of the spores are always lighter in colour than the central ones. This colour difference is least marked in the two strains of *H. sativum* and most pronounced with the strains W_p and *G*. The remaining strains are intermediate in this respect.

A peculiar and characteristic feature of the spores of the strain W_{cp} is that the end septa are thick and dark.

Text-fig. 8.

Text-fig. 9.

Text-fig. 8. *H. sativum* (wheat). 1–16. Oat straw.

Text-fig. 9. Strains W_p and W_{cp}. 1–9. Strain W_p on oat straw. 10–19. Strain W_p on Richards' solution agar (*N*/100). 20–24. Strain W_{cp} on oatmeal agar. 25–30. Strain W_{cp} on prune juice agar.

Apart from the variation in spore length—a variation which obviously affects the *spore shape*—this latter is markedly uniform under different conditions*. Though all the strains may produce a certain proportion of abnormally shaped spores, nevertheless one can associate a certain characteristic shape with the spores of each strain. Groups of spores showing the shapes

* The spores of the strain from ginger vary somewhat from one medium to another. Thus on oatmeal agar and Brown's starch agar the spores are more curved than on Brown's agar or on prune juice agar.

characteristic of the different strains are illustrated in Text-figs. 6–12. All the spores are arranged so that the distal end is uppermost.

Secondary spores. These are formed from the primary spores. The distal cell germinates and on the short germ tube a smaller spore is formed. Sometimes the germ tube is so short that the second spore appears almost as if sessile on the primary one.

Text-fig. 10.

Text-fig. 11.

Text-fig. 10. 1–9. Strain *G* on oat straw. 10–14. Strain *G* on prune juice agar. 15–23. Strain W_{cp} on oat straw.

Text-fig. 11. Strain *P*. 1–12. Brown's starch agar. 13–14. Germination of spores in water.

This process may be repeated, the second spore bearing a third and so on, each successive spore diminishing in size. In this way a chain of spores arises giving an appearance similar to the fructification of *Alternaria*. Occasionally two germ tubes, each of which bears a secondary spore, may thus arise from the distal cell. Such germ tubes have been seen to arise from a middle cell of the primary spore. These secondary spores are usually formed while the primary spore is still attached to the conidiophore.

The proliferation from the spores has been observed in all the strains under study and is a not uncommon feature of the genus.

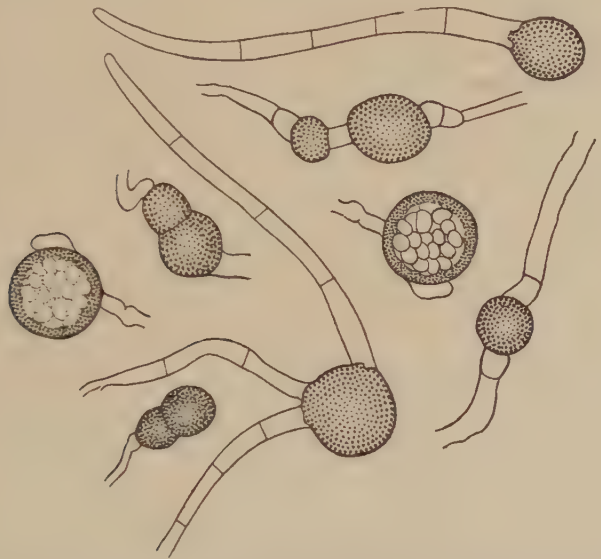
Spore germination. The method of germination is always the same, *i.e.* by the two polar ends, and more usually from the distal end than from the proximal. Rarely germ tubes have been seen to arise from some of the middle cells. Fusions of germ tubes are very common. Germination of spores *in situ* frequently occurs. The conidiophores themselves also very often germinate.

Text-fig. 12. *H. Oryzae*. 1–19. Oat straw.

The spores possess a high degree of resistance to unfavourable conditions. Thus they have been found to germinate freely after long exposure to anaerobic conditions (submersion in water for five months). Similarly a high percentage of viable spores has been found in three years' old cultures on oat straw.

Chlamydospores. When old cultures of any of the strains, especially after cultivation at a somewhat high temperature, are examined, many of the hyphae are found to have a bead-like toruloid structure. It is not certain that these rounded cells with thickened walls can be described as true chlamydospores. True chlamydospores occur in the mycelium and at the tip of aerial

conidiophore-like hyphae of strain W_p when it is grown on Richards' solution agar. These cells are rounded, thick walled, smooth and measure 2–3 μ in diameter. Similar structures are formed by strain W_{cp} on Richards' solution agar but only on the aerial hyphae. Large chlamydospores, 6–20 μ in diameter, were once observed in oat straw cultures of the barley strain of *H. sativum*. Numerous recultures, even on the same medium, have failed to reproduce these structures. These spores germinate readily when placed in water. Text-fig. 13 illustrates the formation of chlamydospores and their germination.



Text-fig. 13. *H. sativum* (barley). Formation of chlamydospores on oat straw culture. Some of them are shown germinating.

F. Infectivity.

Infection experiments were carried out both in India and in England. Those in India were directed to determining whether the strains of *Helminthosporium* in cultivation were parasitic on their respective hosts and whether cross-inoculation of other hosts was possible. The experiments in England were limited to inoculations of wheat and barley with the various fungi under consideration.

(1) *Experiments in India.*

(*a*) *Infectivity of* Helminthosporium *forms on their respective hosts.* Inoculations were carried out by placing suspensions of

spores in water on various parts of the hosts. With strains W_{cv} and *P*, pieces of mycelium were also used as both these strains sporulate feebly. The inoculated plants were kept in moist glass chambers for forty-eight hours, after which they were placed outside in the shade. Uninoculated control plants were similarly treated and remained free from disease throughout. The details of these experiments are given in Table XI. A considerable number of reisolations were made from the infected plants, and the original organism was recovered in each case. Column 3 of the table gives the parts of the host plants on which the inocula were placed.

Table XI. *Inoculation experiments with eight forms of* Helminthosporium *on their respective host plants.*

Fungus	Host	Part of host inoculated	No. of inoculations	No. of infections
W (Pusa)	Wheat	Leaves and leaf sheaths	92	85
,,	,,	Spikelets	15	15
,,	,,	Seedlings	29	26
W (Burma)	,,	Leaves, leaf sheaths and spikelets	42	42
B	Barley	,, ,,	39	39
W_p	Wheat	,, ,,	63	63
W_{cp}	,,	,, ,,	43	37
P	*Panicum frumentaceum*	,, ,,	70	59
G	Ginger	Leaves	203	80
S	Sugar-cane	,,	66	65
R	Rice	Leaves, leaf sheaths, floral parts and seedlings	81	81

From the above table it is clear that all the forms strongly attack their respective hosts, with the possible exception of the strain from ginger, which gave only about 40 per cent. of successful infections on its own host. It will appear below that this is the least virulent of all the forms under study.

(*b*) *Cross-inoculations.* These were carried out in the same manner as described above. The details are given in Tables XII and XIII. The numerator of each fraction gives the number of infections, the denominator the number of inoculations made.

From Tables XII and XIII it is clear that with a few exceptions each of the forms of *Helminthosporium* is able to produce vigorous attack on any of the hosts tested. Though the number of cross-inoculation tests on ginger is limited, it will be noted that this host is definitely infected only by its own parasite.

Table XII. *Cross-inoculation experiments with four forms of* Helminthosporium. (Strains *W*, *B*, W_p and W_{cp}.)

Host	Strains of *Helminthosporium*			
	W	*B*	W_p	W_{cp}
Wheat	166/174	29/36	63/63	37/43
Barley	77/84	39/39	22/31	23/25
Oats	72/85	27/33	14/21	19/21
Maize	32/69	13/29	11/25	14/23
Sorghum	15/58	? 2/20	? 1/25	12/21
Rice	36/55	13/19	12/21	16/19
Sugar-cane	33/82	20/50	24/44	20/36
Eleusine coracana ...	25/25	0/10	—	—
Setaria italica ...	20/20	10/10	—	—
Panicum frumentaceum	19/25	7/10	—	—
Ginger	0/27	? 2/17	—	—

Table XIII. *Cross-inoculation experiments with four forms of* Helminthosporium. (Strains *P*, *G*, *S* and *R*.)

Host	Strains of *Helminthosporium*			
	P	*G*	*S*	*R*
Wheat	—	11/11	37/37	38/42
Barley	—	11/11	18/29	31/37
Oats	—	10/10	28/42	24/34
Maize	15/15	—	48/52	32/44
Sorghum	—	—	23/48	10/28
Rice	—	—	37/37	80/81
Sugar-cane	—	—	65/66	25/31
Eleusine coracana ...	7/7	11/22	—	—
Panicum frumentaceum	59/70	20/26	—	—
Pennisetum typhoideum	—	—	21/30	—
Ginger	0/8	80/203	—	—

(2) *Experiments in England.*

(*a*) *Infection of aerial parts of wheat and barley.* These experiments were carried out in duplicate, one set of plants being kept under bell-jars in the shade and another set in a greenhouse. Forty-eight plants of wheat and the same number of barley were used with each form. Three days after inoculation (by spraying on a suspension of spores in water) all the plants were placed outside in the shade. The results were identical in both sets of experiments. With the two strains of *H. sativum* and with *H. Sacchari* and *H. Oryzae*, the first symptoms appeared after twenty-four hours. Within a week the leaf surface of the host plants showed profuse development of spots. With the other four strains infection appeared more slowly, the first symptoms being seen after two days. Strains *P* and *G* proved to be the weakest of all, the amount of spotting being slight up to the end of the experiment.

(*b*) *Production of foot-rot and root-rot of wheat and barley.* To determine whether the various forms of *Helminthosporium* under consideration could produce the foot-rot and root-rot phases of the disease, experiments were carried out in sterilised test tubes (size $7'' \times 1\frac{1}{2}''$) containing cotton wool soaked with Knop's solution, in Petri dishes, and in pots containing soil sterilised in the autoclave.

All three methods gave similar results.

The seeds before being infected were sterilised with mercuric chloride (1 : 1000) for ten minutes and then washed in several changes of boiled distilled water.

Inoculations were made by placing the seeds or young seedlings in a suspension of spores for ten minutes, after which they were transferred to test tubes, Petri dishes or pots. In order to test soil infection, sterilised soil in pots was well mixed with spores and mycelium, after which sterilised seeds or seedlings were planted. The idea of allowing the seeds to germinate before inoculation was to make sure that all seeds had germinated and that death was due to the fungus. The experiments run in tubes or in pots were kept side by side under similar conditions together with the controls. The advantage of the tube series of experiments was that the course of the disease could be followed without disturbing the plants.

The experiments were repeated nine times with always the same results.

All the forms of *Helminthosporium* with the exception of strains *P* and *G* are capable of producing foot-rot and root-rot of wheat and barley. Strains *P* and *G* give feeble infection and do not produce the typical symptoms of the disease. The comparative degree of infection produced by various forms is illustrated in Tables XIV and XV.

(*c*) *Influence of soil temperature on infection.* The amount of disease produced is materially influenced by soil temperature. The experiments were carried out in the manner already described. The pots were kept in water baths regulated at 20° C., 25° C. and 30° C., the level of the water being maintained about $\frac{1}{2}$–1″ above the surface of the soil in the pots. The soil moisture in the pots was kept as constant as possible by a suitable amount of watering. No attempt was made to secure uniformity of air temperature. A duplicate set of experiments was carried out at the same time in wide test tubes ($7'' \times 1\frac{1}{2}''$). Controls were always kept.

The amount of infection was assessed by a method similar to that given by McKinney (22) and by Nisikado and Miyake (26). According to this method numerical values are assigned to different degrees of attack as follows:

1. No infection ... ... 0·00
2. Very slight infection, as evidenced by small lesions on the coleoptile ... ... 0·75
3. Slight infection, as evidenced by small lesions on the coleoptile or sheath in excess of 2 ... ... 1·00
4. Moderate infection as evidenced by the partial or almost complete rotting of the coleoptile with a few lesions on lower leaf sheath or roots ... 2·00
5. Abundant infection as evidenced by a complete rotting of the coleoptile and numerous lesions on the first internode, lower leaf sheath or roots 3·00
6. Very severe infection, as in 5, and the plants very stunted, dying or killed just after germination ... 4·00

The general degree of infection or "infection rating" is then obtained from the following formula:

$$\text{Infection rating} = \frac{\text{Sum of all numerical ratings} \times 100}{\text{Total number of inoculated plants} \times 4}.$$

It is thus seen that an infection rating of 100 represents the extreme where all the plants of a batch are killed shortly after germination.

Table XIV. *Influence of soil temperature on infection of wheat in terms of infection rating.*

	20° C.			25° C.			30° C.		
Fungus	Seed	Soil	Seed-lings	Seed	Soil	Seed-lings	Seed	Soil	Seed-lings
W	26·7	26·7	29·1	44·0	40·6	43·2	60·5	58·2	64·4
B	28·4	27·9	30·6	52·3	62·5	52·4	67·2	81·2	79·9
W_p	18·8	19·5	20·6	30·5	31·2	30·5	35·4	38·5	40·1
W_{cp}	19·3	19·3	19·3	43·7	43·7	41·7	50·7	51·1	48·1
P	6·0	4·7	7·0	11·6	12·8	14·0	13·3	14·5	15·7
G	7·0	8·6	9·4	12·8	16·0	16·3	15·7	15·7	18·0
S	25·7	25·0	28·1	50·0	53·1	50·0	68·9	73·5	71·9
R	29·2	29·2	29·2	50·0	59·4	53·1	68·7	73·5	75·0

Table XV. *Influence of soil temperature on infection of barley in terms of infection rating.*

	20° C.			25° C.			30° C.		
Fungus	Seed	Soil	Seed-lings	Seed	Soil	Seed-lings	Seed	Soil	Seed-lings
W	32·5	26·6	30·8	52·0	57·5	56·7	71·9	78·0	71·9
B	43·5	39·6	42·9	72·3	67·5	69·9	74·7	73·2	71·8
W_p	23·3	20·5	20·3	45·0	42·9	44·8	63·6	61·5	61·8
W_{cp}	19·3	19·3	19·3	33·6	37·5	34·4	45·3	46·5	50·6
P	7·8	7·0	8·2	12·8	12·8	12·8	15·4	14·5	15·7
G	14·0	12·8	15·7	17·2	20·3	16·8	18·7	19·5	23·4
S	26·1	26·9	26·9	47·2	50·4	56·4	70·3	70·3	75·0
R	31·2	37·5	42·2	50·0	61·0	59·4	73·5	78·1	78·1

The average results obtained from six experiments are shown in Tables XIV and XV in terms of infection rating. The results obtained in the pot and test tube experiments were closely similar as regards the kind and degree of infection.

The figures obtained show that both wheat and barley seedlings can be infected by any of the species under consideration and that all except strains *P* and *G* are capable of causing pronounced foot-rot and root-rot. Further it will be noted that the amount of infection strongly increases as the temperature is raised from 20° C. to 30° C. Infection experiments were also carried out at 35° C. At this temperature seed germination is poor and the amount of infection is also very slight.

From the results of the inoculation experiments, it is clear that all forms are capable of attacking a wide range of hosts, at least under artificial conditions of inoculation. The question thus arises why these forms are not found on other hosts in nature. This point is not clear at the moment and will require further investigation. It is possible that some overlapping does occur and that evidence of this may be obtained if sought for in the right place. For example, careful examination should be made where two crop plants are growing side by side to see whether the stripe-producing organisms are strictly limited to their respective hosts. One would also have to bear in mind that conditions of cropping, season, perennation of the fungus, etc., might underlie the specialisation known to occur. On the other hand, the explanation may lie in the possibility that artificial inoculations are not an absolute test of what will happen in nature, as the conditions are in general more favourable for attack.

G. Specific identity of various forms of *Helminthosporium*.

The general conclusions are that macroscopic growth features are practically valueless in delimiting species of *Helminthosporium* within the range of the eight forms under consideration. The criterion of pathogenicity is also of little value, as it has been shown that most of the forms freely attack a wide range of host plants, at least under artificial conditions of inoculation.

One is reduced therefore to the consideration of microscopic characters. Some of these also are variable, *e.g.* spore size and degree of septation. These vary not merely among the different strains which arise by saltation* from a parent but with any one of these under different growth conditions. The range of spore size and septation therefore must be made so wide as to include the saltant forms, and one will require in general to give the

* An account of these will appear in a future number of the *Transactions*.

data in reference to certain standardised media under standard conditions. Spore size and septation are definitely characters of specific value, but must not be interpreted too narrowly.

From an extensive study of the growth features of the eight forms under consideration and of the saltants derived from them, it can be stated that certain features of the spores are markedly constant. One such feature is the shape. Apart from the variation in shape which follows naturally from variation in length, there is a high degree of constancy shown as regards the sharpness or bluntness of the ends and the position of the region of greatest diameter of the spores. Thus the two strains (*W* and *B*) of *H. sativum* as found in nature are characterised by spores with rounded ends and with the region of maximum width half-way to one-third from the base. These features are shown distinctly in all the modifications of those forms which arise under different environmental conditions and in all the saltant strains which have been isolated. Similarly the characteristically pointed proximal end of the spores of strains W_{cp} and *P* is shown under all the cultural conditions to which these strains have been subjected.

A like degree of constancy is seen in the colouring of the spores. For example, the spores of strain W_p are distinctly darker than those of the two strains of *H. sativum* (*W* and *B*) under all cultural conditions. This is so also in all the saltants.

In strain W_{cp} the end septa are thicker and darker than the others. This feature has proved to be constant under all conditions and is not shown by any of the other forms, parent or saltant.

The delimitation of the species must therefore be on the basis of such characters as the above. Bearing these points in mind one can arrive at a decision as to the specific identity of the forms examined in this work. The general respects in which the different parent forms together with their saltants are characterised are as follows.

(1) *and* (2). H. sativum *Pamm. King & Bakke on wheat and barley.*

The spore size in culture is 16·5–102·5 μ in length and 13–26·5 μ in width, the average being 75 × 21·5 μ. Some strains may range in width even up to 30 μ. Septation is 0–10 with an average of 6·5. The spores are typically spindle-shaped and sometimes slightly curved, broadest between the base and the middle, and tapering towards the ends which are rounded off abruptly. They are yellowish brown to dark olivaceous, often with a bluish green tinge. The end cells sometimes have a paler spot, and on certain media are slightly lighter. The episporium is fragile.

Spores of smaller size and lower septation are often present both in the parent form under certain conditions of growth or as permanent features in some strains. Such spores are reduced to sub-spherical bodies, often non-septate or with a single cross wall. Irregular twisted and bilobed spores are often present, but such bilobed spores have also been noticed in other species of *Helminthosporium*.

H. sativum was originally described by Pammel, King and Bakke (31) and since then much work has been done on it, especially by Stevens (33), Christensen (6, 7), Dosdall (11) and others. Differences in detail as recorded by the various authors are probably due to environmental conditions under which the fungus was grown. The variation in size and septation of the spores of this species has also been observed by Christensen (6, 7) and by Dosdall (11).

The two strains, one (*W*) from wheat and the other (*B*) from barley, agree closely with the descriptions of Stevens (33) and Drechsler (12). The variations in spore length, width and septation are shown in Tables VIII and IX (see under *W* and *B*). Typical spores showing the range of variation are illustrated in Text-figs. 6–8. Both Indian strains have been compared side by side with a typical American strain of *H. sativum** and found to be in essential agreement.

(3) *Strain W_p on wheat.*

This form though occurring on wheat cannot be allocated to *H. sativum*. It is clearly distinguishable from it by the following features: spores are narrow, more cylindrical, and darker in colour (they may be quite opaque), while the end cells are light to subhyaline. As compared with most strains of *H. sativum* the spores are shorter and less septate.

It does not resemble any other known species on wheat or on any other grass, and therefore a new name is proposed.

Helminthosporium bicolor, n. sp. Conidiophores of *H. sativum* type, but dark greyish brown. Conidia typically cylindrical with abruptly rounded ends, sometimes slightly broader in the middle; straight or very slightly curved; 1–9 septate (average 5), the body of the conidia greyish to dark greyish smoky brown, sometimes quite opaque, the two end cells lighter, sometimes subhyaline. Extreme measurement 16·5–79 × 10–20 μ (mean 51 × 14 μ).

Associated with foot-rot of wheat in Poona, India.

The variation in spore length, width and septation of this

* The writer wishes to acknowledge his indebtedness to Dr J. J. Christensen, of Minnesota University (U.S.A.), for kindly sending a culture of typical *H. sativum* and also comparing it and confirming the identification.

fungus is shown in Tables VIII and IX (see under W_p). Irregular types of spores such as bilobed are also found. Text-fig. 9 (nos. 1–19) illustrates the variation in spore shape and septation.

(4) *Strain W_{cp} on wheat.*

This form, like the one already described, though occurring on wheat cannot be placed with *H. sativum*, the spores being easily distinguishable as follows:

H. sativum	Strain W_{cp}
Both ends abruptly rounded off	Distal end abruptly rounded off, proximal end somewhat pointed
All the segments concolorous, apart from a paler spot at each extremity	End cells distinctly lighter than intermediate ones in the majority of spores
Septa all alike	Distal and proximal septa conspicuously deeper than the intermediate ones

The range of spore length and width of strain W_{cp} is also much inferior to that of *H. sativum*.

The fungus showing the closest resemblance to strain W_{cp} is *H. halodes*, described by Drechsler (12) on *Distichlis spicata*, which has the same sporal features. It differs as regards spore size and septation as follows:

Fungus	Spore length	Spore width	Spore septation
H. halodes	20–103 μ	10–14 μ	1–12
Strain W_{cp}	23–73 μ	13–20 μ	2–9

Since spore measurements and degree of septation vary considerably under different environmental conditions it is considered that strain W_{cp}, though it may not be identical with *H. halodes*, is however very closely allied to it. Hence the name *H. halodes* Drechs. var. ***Tritici*** nov. var. is proposed.

Helminthosporium halodes Drechs. var. ***Tritici*** nov. var. Conidiophores as in the main type. Conidia cylindrical or elliptical with distal end abruptly rounded off and proximal end showing a more perceptible tendency to taper to an acute point. The basal cell is somewhat triangular and at its tip has a prominent hilum which slightly protrudes. Conidia widest near the middle, straight or slightly curved, 2–9 septate (average 6), the distal and proximal septa being conspicuously darker and apparently thicker than the rest; the body of the conidium light greenish brown to brown or smoky brown, the two end cells, especially the basal, being slightly lighter. Extreme measurement, 23–73 × 13–20 μ (mean 52 × 16·5 μ).

Associated with foot-rot of wheat (Central Provinces, India).

The variation in spore length, width and septation is shown

in Tables VIII and IX (see under W_{cp}). Irregular types of spores such as bilobed are not uncommon. Sometimes spores with the widest part near the distal end are also seen. Text-fig. 9 (nos. 20–30) and Text-fig. 10 (nos. 10–23) illustrate the variation in spore shape and septation of this fungus.

(5) *Strain P on* Panicum frumentaceum.

This form is different from any of the species described on *Panicum* or any other graminaceous host. The list of *Helminthosporium* species known to occur on *Panicum* is as follows:

H. Crus-Galli Nisikado and Miyake on *P. Crus-Galli,* which according to Nisikado and Miyake (27) is identical with *H. monoceras* Drechs.

H. Panici Overeem (37) on *P. maximum.*

H. Panici-milacei Nisikado (25) on *P. miliaceum.*

H. Yamadai Nisikado (25) on *P. miliaceum.*

H. flagelloideum Atk. and *H. ustilaginoideum* Sacc. on *Panicum* sp.

The spores of strain *P* are entirely different in shape from those of the last five, but somewhat resemble those of *H. Crus-Galli* (*H. monoceras*) in general shape. They differ however in being much narrower, in being thin walled and in having a much lighter colour. Strain *P* was compared with a culture of *H. monoceras* sent by Dr Christensen and found to differ as described above. Drs Christensen and Dosdall (personal communication), from a study of a culture sent to America, also agree that strain *P* represents a new species.

Helminthosporium frumentacei, n. sp. Conidiophores of *H. sativum* type, 62–263 × 4·5–7·5 μ, brown to dark brown. Conidia typically fusoid, straight or slightly curved with rather a rounded distal end and tapering to an acuminate base which bears a prominent hilum, thin walled, yellowish to light olivaceous or light brown, all cells except the apical and basal with granular contents; 3–11 septate (average 7), measuring 49–158 × 10–18·5 μ (average 110 × 15 μ).

On leaves and leaf-sheaths of *Panicum frumentaceum* at Pusa, India.

The variation in spore length, width and septation is shown in Tables VIII and IX (see under *P*). Text-fig. 11 illustrates the type of spores.

(6) *Strain G on ginger.*

The conidia are cylindrical, elliptical or lunar shaped, the last type predominating. Curvature of the spore is especially marked on certain media such as oat straw, oatmeal agar, Brown's starch agar and prune juice agar. The conidia are usually widest

in the middle and gradually taper to rounded ends, and light olivaceous or dark brown to opaque. The end cells are generally of lighter colour, a feature especially well marked on certain media such as oat straw, oatmeal agar, prune juice agar or Brown's starch agar. Even in the darker or opaque type of spore the end cells may be subhyaline. Occasionally in conidia of the straight type the widest part may be near the base. Irregular or bilobed types also occur. In size the conidia are 30–115·5 × 11·5–20 μ (average 77 × 14 μ), 1–11 septate (average 6).

No *Helminthosporium* has been previously recorded from ginger. Strain *G* closely resembles *H. Maydis* Nisik. & Miy. (= conidial stage of *Ophiobolus heterostrophus* Drechsler (13)) in size and septation of spores as may be seen from the following.

Fungus	Spore length	Av. length	Spore width	Av. width	Spore septation	Av. septation
H. Maydis	22·9–112·2 μ	75·0 μ	8·9–17·8 μ	13·6 μ	0–10	6·68
Strain *G*	30–115·5 μ	79·9 μ	11·5–20 μ	14·1 μ	1–11	6·05

The chief difference is that the spores of strain *G* have distinctly lighter end cells on most media, a fact which has not been mentioned either by Nisikado and Miyake or Drechsler. However, an examination of the illustrations of Nisikado and Miyake (28,23) shows that some of the spores have light coloured end cells. Moreover, a comparison of strain *G* with a culture of *H. Maydis* sent by Drechsler showed a close agreement between the two forms. The behaviour of strain *G* when inoculated on maize has not yet been tested, but even should it prove to be non-pathogenic, in the light of experimental work carried out with these forms, such a difference should not be accorded specific value. It is proposed therefore to assign strain *G* to *H. Maydis* with the reservation that it may prove to be a strain different from that occurring on maize.

The variation in length, width and septation of spores of this strain is shown in Tables VIII and IX (see under *G*). Text-fig. 10 (nos. 1–14) illustrates the variation in spore shape and septation.

(7) H. Sacchari *Butl. on sugar-cane.*

An extensive study of *H. Sacchari* Butl. shows that the description as given by Butler and Hafiz (5) requires some revision. The spore size as given by these authors is 35–60 × 8·5–12 μ, but from a study of naturally occurring material the writer gives the measurement as 32–120 × 11–17 μ. Leaf spots showing spores of smaller size have been found when incubated to produce a longer type of spore.

The study of the effect of environment has shown that spore

size is greatly affected by temperature. The temperature in Pusa (India) ranges from about 15° C. to about 40° C. according to the time of year and this fact probably explains the discrepancy in results. Again the study of saltants has shown that this species consists of several strains which differ considerably in range of spore length and width. The following is a description of this fungus:

The conidia are cylindrical, long elliptical and generally slightly curved, the prevalence of curved spores varying in different media. The conidia are generally widest in the middle, gradually tapering to rounded ends, yellowish, light olivaceous to dark smoky brown with often a tinge of greenness. The end cells are often slightly paler. In size the conidia (in culture) range from 30–112 × 11·5–18·5 μ (average 68·3 × 15·3 μ) and are 3–11 septate (average 6·9). The species consists of several strains, some with shorter and others with longer spores. For example, in one long-spored strain, the average length is 81 μ and the average degree of septation is 8·4.

The variation in spore size and septation for the parent strain is given in Tables VIII and IX. Text-fig. 7 illustrates the shape and septation of spores on different media.

(8) H. Oryzae *Br. de Haan on rice.*

Strain *R* from rice agrees in general with the descriptions of *H. Oryzae* given by various writers such as Nisikado (24). Such discrepancies as exist can readily be set down to the effect of environmental conditions or to the existence of a number of strains within the species. A general description of this species is as follows:

The conidia are long elliptical or obclavate and generally curved to one side (especially on certain media). They taper to rounded ends, the maximum width being between the middle and the basal end, and sometimes at the middle itself. The colour is light greyish olivaceous to greenish brown, the end cells and especially the basal cell being sometimes lighter. The range of spore size is 30–172 × 10–23 μ (average 88 × 17 μ), and the degree of septation is 2–16 (average 6·7). The species consists of several strains, some with shorter and others with longer spores. For example, in one long-spored strain, the average length is 123 μ, average width 21 μ, and the average degree of septation is 9.

The variation in size and septation of the spores of the parent strain is shown in Tables VIII and IX. Text-fig. 12 illustrates the shape and septation of the spores of the parent strain.

Summary.

1. Seven species or strains of *Helminthosporium* occurring on various cultivated grasses and one on ginger have been studied.

2. The symptoms of disease as seen in nature together with the morphology of the various forms under natural conditions have been described.

3. The eight fungi used were studied under different conditions of growth in artificial culture. The following were the main results:

(*a*) Rate of growth depends on a number of factors, such as type of medium, amount of medium, presence or absence of light. There are certain strains, *e.g.* that from ginger, which show a slow growth-rate under all conditions tested.

(*b*) The effect of temperature on growth also depends somewhat on the nature of the medium. The eight fungi show a certain amount of differentiation as regards the position of the optimal and maximal temperatures for growth and as regards sensitiveness to heating.

(*c*) The macroscopic features of growth were found to vary very considerably. Details of the effect of cultural conditions on amount of aerial mycelium formation, colour formation, zonation, etc., are given in the text.

(*d*) Certain microscopic growth features show a greater degree of constancy. Though amount of sporulation and spore measurements vary a good deal, spore shape and colour are markedly constant and therefore are of value for specific delimitation.

4. An extensive series of inoculation experiments was carried out with the following results:

(*a*) Each fungus freely parasitises the host plant from which it was isolated.

(*b*) Under artificial conditions at least, most of them are able to infect a number of hosts other than their own.

(*c*) With the exception of two strains, all are able to produce the root-rot and foot-rot phases of disease in wheat and barley.

(*d*) The intensity of the foot-rot and root-rot disease produced is markedly influenced by soil temperature, being greatest when the latter is in the neighbourhood of 30° C.

(5) Of the eight forms studied, two have been assigned to new species. These are named *Helminthosporium bicolor* and *Helminthosporium frumentacei*. A strain from wheat is considered to be a variety of *Helminthosporium halodes* Drechs. and the strain from ginger to be *Helminthosporium Maydis* Nisikado and

Miyake or a variety of the latter. The other forms are assigned to species already described. In the particular case of *Helminthosporium Sacchari* an amended diagnosis is given, with special reference to the size of the spores.

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EXPLANATION OF PLATE IX.

Fig. 1. Wheat leaf affected by *H. sativum*.
Fig. 2. Leaves of *Panicum frumentaceum* affected by strain *P*.
Fig. 3. Leaves of ginger affected by strain *G*.
Fig. 4. Cultures of three strains of *Helminthosporium* from wheat and one from barley on sterilised rice showing scattered patches of tufted growth giving appearance of sclerotia. (From left to right *B*, *W*, W_p, W_{cp}.)

SPORES AND SPORE GERMINATION IN THE GENUS PHYTOPHTHORA.

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(With 7 Text-figures.)

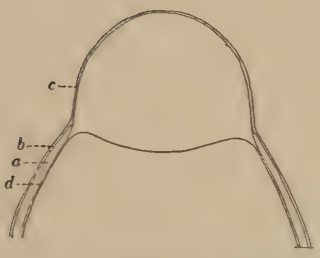
I. Spores.

There are many kinds of spore, produced by species of *Phytophthora*, though perhaps not quite so many kinds as there are names for. The following have been recognised:

(*a*) the conidium or sporangium,
(*b*) the sphaero-conidium,
(*c*) the resting conidium,
(*d*) the chlamydospore,
(*e*) the oospore (by fertilisation),
(*f*) the parthenogenetic oospore.

Conidium. The conidium is borne, as a rule terminally, on a slender hypha, either under water as recorded by Pethybridge (1913) for *P. erythroseptica*, or aerially in a moist atmosphere as in the majority of species. It is inversely pear-shaped, with a papilla, and its size is variable. It may occasionally be intercalary (Text-fig. 6). The wall appears to be formed of three more or less distinct layers. Except at the papilla the middle layer (Text-fig. 1 *a*) becomes firm, resistant and inelastic; it is, moreover, not readily stained. No doubt it is the extreme development of fungus cellulose. This is the layer that survives long after germination. It is the persistent layer of dead or empty sporangia. Outside it there sometimes can be demonstrated a very thin layer which is continuous as an easily broken pellicle over the papilla (Text-figs. 1 *b*, 2). The outer layer of the papilla is very thin, but it may be double (Text-fig. 1 *c*). It stains readily: black with nigrosin and blue with cotton blue. The innermost layer of the wall, except at the papilla, is very thin and appears to be continuous with the thickened region that forms the body of the papilla, for in young conidia both regions are easily stained with ruthenium red (Text-fig. 1 *d*). The number of nuclei varies with the size of the conidium: larger conidia having more nuclei. As Dastur (1913) has so well described for *P. parasitica* and Butler (1913) for *P. Colocasiae*, there may be a vacuole in the immature conidium which disappears on formation of zoospores. This is a sap vacuole and must not be confused with the oil vacuole of the older conidium.

Germination takes place either directly by a tube, or indirectly by the liberation of zoospores which swim for a while by the aid of two unequal cilia and then settle down and germinate by a tube. The zoospores may first be expelled as a mass into a thin vesicle, through which they finally break and swim away (Text-fig. 3). Sometimes the mass appears to be pressed out



Text-fig. 1. Papilla of conidium of *Phytophthora Cactorum* showing wall layers.

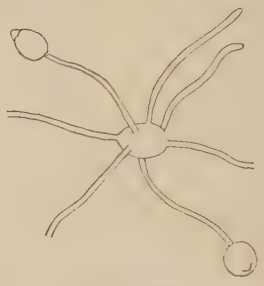
Text-fig. 2. Conidium of *P. Cactorum* empty of zoospores which have escaped through an aperture below the papilla.

Text-fig. 3. Development of vesicle in *Phytophthora Colocasiae.*

by an inner vesicle, or again the zoospores may be seen swimming freely within the sporangial wall before escaping singly. Occasionally the zoospores escape through a rupture in the thin part of the wall just below the papilla, pushing aside the papilla which has apparently begun to undergo those chemical processes that prevent it from swelling into a vesicle (Text-fig. 2). Most frequently the final separation of the uninucleate zoospores takes place outside the conidium, which must now be termed "sporangium."

Sphaero-conidium. The sphaero-conidium first described and figured for *P. parasitica* by Lafferty and Pethybridge (1922) is usually intercalary though it may be terminal. It is borne on

a stouter hypha than that which gives rise to a conidium and from it grow slender hyphae which are not always germ tubes. Germ tubes may, however, grow out, giving rise to conidia or further sphaero-conidia. Rosenbaum (1915) and Rose (1924) have reported that they found sphaero-conidia appearing in old cultures of *P. Cactorum* and we have confirmed this observation Text-fig. 4). We have since found them in old cultures of *P. parasitica* and *P. cryptogea*.

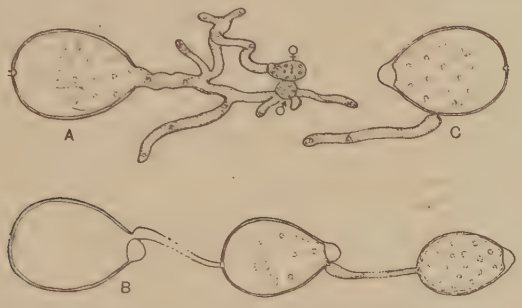


Text-fig. 4. Sphaero-conidium of *Phytophthora Cactorum* from an old culture.

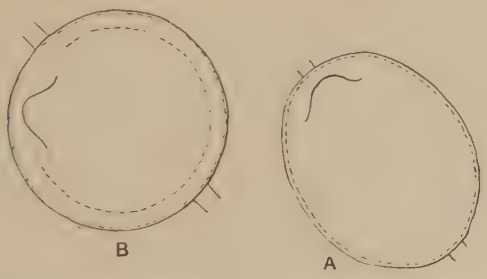
Resting conidium. This term is used for two apparently different bodies which, however, may ultimately prove to be identical. In *P. Cactorum*, for example, the resting conidium is formed in the same way as the ordinary conidium—indeed in the early stages of development it *is* a conidium which might, if germinated early enough, produce either zoospores or a tube. But on a slowly drying medium it may persist for weeks or months slowly undergoing metabolic change, firstly accumulating a fatty reserve and finally living on this until it seems that it needs must put out a tube. On the same medium, exhausted of food supply and rich in its own staling products, it may produce only a very short hypha and then a conidium again, which may repeat this story passing through the same maturation phases until it too must germinate, thus forming a chain of conidia, each smaller than the last, as a certain amount of reserve has been used up at each germination. These so-called "chains of conidia" have often been described as occurring in old cultures; Dastur (1913) adds "and in those not kept in pure water." Gadd (1924) claims that germ tubes from conidia give secondary conidia in absence of plentiful food. Resting conidia of *P. Cactorum*, germinated in a fresh medium, may give rise however to vegetative hyphae, or sporangia, or sexual organs (Text-fig. 5). The resting conidium described by Dastur (1913) is what other workers call a chlamydospore.

Chlamydospore. This body is spherical and is characteristically, though not always, without a papilla (Text-fig. 6 B). It is borne terminally or is intercalary and is extremely variable in size within the one strain. It develops a thicker wall than is ever formed by the resting conidium, it can rest for a longer period and probably can resist a higher temperature. Dastur (1913), who does not recognise any real difference between "resting conidium" and "chlamydospore," gives a very detailed account of the chemical reactions of the three-layered wall. The chlamy-

dospore develops a big oil reserve stored in a central vacuole which breaks up preliminary to germination. Thin places, germ pores, can sometimes be seen in the wall. After digesting its innermost wall, and absorbing its store of fatty reserve, it germinates by putting out one or two germ tubes much in the manner of an oospore. One or other of the tubes soon produces a



Text-fig. 5. Germination of resting conidia of *Phytophthora Cactorum*.
A. Mycelium producing sexual organs immediately. B. Chain of resting conidia from an old culture. C. Germ tube emerging through a germ pore (cf. chlamydospore).

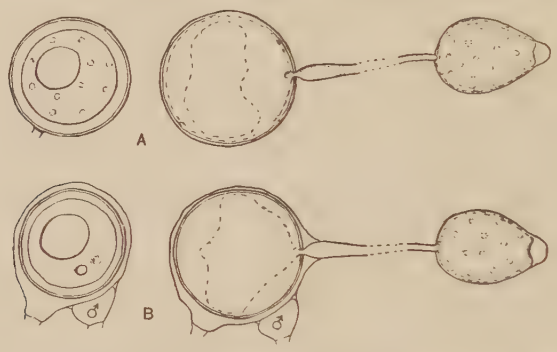


Text-fig. 6. A. Intercalary conidium of *Phytophthora Cactorum* (conidia are usually terminal and always have a papilla). B. Intercalary chlamydospore of *Phytophthora parasitica* with papilla (chlamydospores are usually without papilla and often terminal). Wall thickness indicated by dotted lines.

conidium (= sporangium) (Text-fig. 7 A). Except for the absence of an oogonium wall with its firmly attached antheridium it is impossible to distinguish an old germinating chlamydospore from an oospore (Text-fig. 7 B).

Oospore. The oospore can always be distinguished with certainty by the persistent oogonium wall around it and the persistent antheridium at its side. The *unripe oospore* is considerably smaller than the oogonium which produced it. It has a very thick three-fold wall, which has been described by Murphy

(1918) for *P. erythroseptica*, dense protoplasm with a fusion nucleus, a large vacuole with an oily reserve, and a small refractive body close to the nucleus which may be an elaioplast. The *ripe oospore* may be found in culture from six to twelve months later and perhaps even earlier and later than this. The process of maturation involves (1) the breaking up of the large vacuole into small and smaller ones until they finally disappear from the protoplasm and the oospore no longer turns black with osmic acid, (2) the digestion and absorption of the innermost layer of the wall, (3) the disappearance of the refractive body, which probably means the subdivision of the elaioplast, (4) the division of the large fusion nucleus into a large number of small



Text-fig. 7. A. Germinating chlamydospore of *Phytophthora parasitica*. B. Germinating oospore of *Phytophthora Cactorum*.

nuclei. It is at this stage that the oospore looks very like the ripe chlamydospore (also a multinucleate body) and in the same way puts forth one or two germ tubes one of which usually bears a conidium (= sporangium) (Text-fig. 7).

Parthenogenetic oospore. Pethybridge (1913) and Szymanek (1927) have reported parthenogenetic oospores, *i.e.* resting spores which look like oospores but which have no antheridium at hand, and both workers figure these oospores showing the oogonium wall outside. Otherwise the body might have been called a chlamydospore.

II. Conditions of germination.

Conidia. Concerning the germination of these spores, by far the greatest interest has been taken in the conidium; chiefly no doubt because of the two methods possible, viz. the indirect, *i.e.* by zoospores, and the direct, *i.e.* by a tube.

Water. It was de Bary (1863), working on *P. infestans*, who

first described the germination by zoospores. His observation was that when fresh, ripe conidia were placed in water the protoplasm separated into portions which issued in a swelling gelatinous membrane at the top. He further observed that if the conidia were "disturbed by any cause" and prevented from giving zoospores, the same conditions induced direct germination. Ever since that time workers have agreed that water is the most obviously necessary external factor required to bring about germination.

Oxygen. Before 1910 Klebahn germinating sporangia of *P. Syringae* stipulated that this fresh water supply must be charged with oxygen. Five or six years later Robinson (1915) for a species on diseased asters recommended "fresh, well aerated water"; Gadd (1924) observed that air was "a most important factor and not always sufficiently recognised"; and Hopkins (1925) claimed to have produced zoospores from sporangia in "fresh aerated water." It was generally assumed that oxygen was a second necessary external factor. In 1926 Uppal made a series of very careful experiments on *P. Colocasiae*, on the need for oxygen in germination. Sometimes he exhausted the small chamber by means of a vacuum pump, sometimes he removed the oxygen by using alkaline solutions of pyrogallic acid, and always used boiled water; the astonishing fact was revealed that whereas air is necessary for the production of a germ tube, it is not necessary for the production of zoospores. Uppal suggests that the liberation of zoospores is nothing but a rearrangement of protoplasm, while the production of a tube involves growth and needs energy.

Certain observations we have made on germination of conidia borne on submerged and therefore poorly aerated mycelia should be examined in this connection, as they do not point to oxygen as more necessary for direct than for indirect germination. The experiments were made with pieces of mycelia of *P. palmivora* cut out from an agar plate and kept submerged in water. During two days' continuous submergence some conidia were found to have germinated by tubes. Part of this mycelium was then irrigated with fresh water (*i.e.* aerated water) and some conidia gave zoospores after fifty or sixty minutes. During three days' continuous submergence it was found that many conidia had germinated by tubes and given secondary conidia. On irrigation with fresh water no germination by zoospores was obtained.

Light. Light was one of the first factors to be taken into account. In 1910 Coleman working with *P. Arecae* demonstrated that whereas zoospores were emitted in ten to fifteen minutes in the light, the conidia remained intact for a month or more in the dark and then, rarely, gave a tube. Three years later Dastur

(1913) showed a similar difference to hold for *P. parasitica*, although he reported a more ready germination by tubes in the dark. He says: "Light seems to influence the formation and emission of zoospores," and after comparing a dozen hanging drop cultures kept in a dark cupboard with a dozen on the bench in ordinary daylight he reports: "Within half an hour all the mature sporangia in the cultures left on the bench had discharged their zoospores while there was no change in those kept in the dark; but the next day sporangia in these cultures had germinated conidially." Gadd (1924) claims that more zoospores are produced in the light than in the dark. We have nothing further to report. Any observations we have made on germination in absence of light have been open to the criticism that other factors, *e.g.* temperature and fresh water supply were influencing the operation. But it seems clear that light, so far as it influences germination at all, determines rather the method of germination than the process itself; in other words, not whether germination will take place or not, but in which way it will take place.

Temperature. Temperature seems to control the method of germination as well as being a limiting factor in germination itself, for however suitable the water supply, unless the temperature is above a certain minimum and below a certain maximum, germination of any conidium will not take place. Melhus (1915) working on *P. infestans* observed that the time required for germination varies with the temperature and that temperature affects the method of germination, and suggested that the explanation should be sought in the greater energy required for the production of a tube than for the production of zoospores. But there appears to be a different optimum for the germination of the conidium by zoospores from that for germination by a tube. Jones, Giddings and Lutman (1912) gave for *P. infestans* the optimum for zoospore production as lying between 10° and 20° C.; for germ tubes round about 25° C. Melhus's observations (Tables I and II), Murphy's (1922) and Vowinckel's (1926) on this same species support these figures. Butler (1913) found a similar difference to hold for *P. Colocasiae* and Uppal (1926) confirmed this; but Uppal gives higher optima: 10°–25° C. for zoospores; 25°–32° C. favouring tubes. Higher optima too are given by Gadd (1924) for *P. Faberi*: 20°–25° C. for zoospores. Now Uppal worked in Iowa and Gadd in Peradeniya where the normal temperature of the working day is already high: Uppal states that his bench temperature was 22°–23° C., and Gadd says: "normally the (room) temperature varied between 24° and 27° C."; and these higher optima coupled with a higher normal temperature suggest that it is not the number of degrees centigrade that is important but rather the temperature relative to

the normal, provided that the temperature lies within the required limits. That it is a common practice in the tropics to drop ice into the water in order to encourage zoospore formation, may be explained by the fact that the temperature is above the maximum for zoospore production.

Table I. *Germination of conidia of* Phytophthora infestans.

(% obtained by estimating the *number of slides* which showed germination. Conidia removed into water drops on slides and placed in moist Petri dishes at various temperatures.)

Temperature in ° C.	0–1	2–3	5–6	8–9	10–11	12–13	14–15	16–17	20–21	24–25	29–30
No. of slides examined	47	18	41	28	117	47	56	22	58	27	45
Time in hours	18	8·7	3·8	3	2·2	1·8	2·8	3	6·2	6·7	24·3
% germination	0	33	100	100	100	100	80	68	38	37	0

Table II. *Germination of conidia of* Phytophthora infestans.

(% obtained by counting the number of conidia in a given area.)

Temperature in ° C.	5–6	10–13	17–18	20–21	22–23	26–27	28–30
% direct germination	0	0·8	13	18	25	14	0·2
% indirect germination	55	80	27	14	1·4	0	0
% no germination	45	19	59	67	73	85	99

Tables I and II are summaries of tables from Melhus, I. E., "Germination and infection with the fungus of the late blight of potato: *Phytophthora infestans*," Agric. Exp. Sta. Univ. Wisconsin Res. Bull. 37 (Aug. 1915).

As long ago as 1911 Melhus, observing the production of zoospores in other members of the Peronosporales, viz. *Cystopus*, *Plasmopora* and *Peronospora*, claimed to show the favourable effects of chilling. However (1915) he could show no such effect for *P. infestans*, but he noted here that in nature germination by zoospores takes place in the early morning dew, not so germination by tubes. In connection with this observation three facts should be borne in mind. Firstly we must take into account what happens in cultural work when the Petri dish containing the fungus is removed from the incubator (temperature 23° C.) to the bench (temperature 10°–15° C.). The immediate effect on a young culture is to induce germination of conidia by zoospores or more rarely by a tube. This may be a direct result of the chilling, but it may be an indirect result and actually due to the condensation of water in the Petri dish causing pure aerated water to fall on the conidia. Perhaps this is the part played by the early morning dew referred to by Melhus, although he says: "The fall in temperature which leads to the deposition of dew and thus provides a medium in which the zoospores may develop, serves at the same time as the necessary stimulus to the ger-

mination of the conidia." Secondly it must be remembered that fresh conidia are probably formed in the early morning, *i.e.* the conidia under observation are young conidia and more likely therefore to germinate by zoospores. Thirdly the temperature may be actually rising from below the minimum towards the optimum when germination takes place in the early morning.

So far, then, it appears that temperature may affect germination in three ways:

(1) As a limiting factor in the germination of conidia supplied with fresh aerated water.

(2) As a determining factor in the method of germination: giving different optima for germination by zoospores and germination by a tube (always provided that other conditions internal and external are suitable for either method).

(3) Acting indirectly: a sudden cooling causing condensation and, as a natural consequence, germination in the fresh aerated water so supplied (unless it is that a too high temperature has been lowered to within the limits requisite for zoospore production).

But this still leaves unexplained the higher optimum. Why should a higher temperature stop zoospore formation and yet allow of tube formation? There may be yet a fourth way in which temperature can control germination and that is in hastening the maturation of the conidium. The production of a conidium (= sporangium) and the liberation of zoospores may be a matter of a few hours only; but for the ripening of a similar spore so that it may germinate by a tube either of two conditions appears to be essential: a longer period at the same temperature or a higher temperature for a shorter period of time. When in 1911 Melhus recorded his observation that cooling was necessary for the germination of conidia of the Peronosporales he stated that the "time of year had a direct effect on the time required for germination": that the average length of time required to induce germination was three and a half hours in August, seven and a half hours in September and nine hours in October and he adds that the cause of this increase in time is not determined. In 1915 he made careful experiments on germination of conidia of *P. infestans* and showed that the time required to bring about germination in water varied according to the temperature; that at a low temperature (down to a minimum of 2°–3° C.) and at a high temperature (up to a maximum of 25° C.) germination was slow to take place, but that at an optimum of 12°–13° C. it took place quickly (Table I). Is this optimum temperature perhaps just the one at which the metabolic processes can best be speeded up? The conidia in the cultures would be in varying stages of development when the

experiments began. It is possible that some were just ripe and ready to germinate by zoospores and others were young enough to be induced to germinate by zoospores, but that others had already passed beyond that stage and were maturing from the sporangial state with its active protoplasm, to the conidial state with its weight of reserve foods. The additional temperature accelerated this, probably chemical, process and germination by tubes then took place. On the other hand a lowering of the temperature might mean condensation and in this film of fresh water the conidia might be caught in a sufficiently early phase of maturation so that zoospores could form, though not so quickly as in a young "sporangium." This offers an explanation for the longer time which elapses before germination in older conidia.

Maturation. From time to time it has been held that the age of the spore must be taken into consideration; in other words, that the proper maturation of the spores is very important. McAlpine (1910) referring to conidia of *P. infestans*, said: "It is found that the first crop of sporangia produces zoospores while later crops are variable in this respect. It is very probable that if sporangia are constantly supplied with moisture they are certain to produce zoospores, but if dried up for even a very short time and again become moist they do not produce zoospores." Rosenbaum (1915) after numerous attempts to germinate conidia suggested that age has more to do with manner of germination than external conditions. Murphy (1922) stated that the tendency to produce tubes is "in the conidia themselves." A consideration of age offered an explanation of behaviour which other factors failed to explain.

It is impossible to distinguish among fresh conidia which will give zoospores and which tubes, but the age of the mycelium bearing the conidium may be of importance in this connection. When Rosenbaum (1915) suggested that the age of the conidium of *P. Cactorum* influenced the method of germination, he said that cultures just beginning to form conidia are more likely to give germination by zoospores. In 1917 he made a comparative study of various species of *Phytophthora* grown under similar conditions and came again to the conclusion that the age of the culture must be taken into consideration. Uppal (1926) found that all conidia of *P. Colocasiae* germinated by zoospores provided that the culture was not older than seven days. Ashby (1929), referring to the germination of conidia of *P. palmivora* by zoospores, wrote: "The proportion lessened as the age of the cultures increased."

Table III is a summary of similar observations we have made on *P. Cactorum* and it shows clearly the influence of age on

Table III. *Germination of conidia of* Phytophthora Cactorum.

	Age of culture in days	Total no. of conidia	% giving zoo-spores	% germi-nated by tubes	% not germi-nated	Method
1	4	45	89	—	11	Scraping
2	9	238	94	—	6	Surface section
3	10	175	96	—	4	,, ,,
4	6	63	76	—	24	Scraping
5	6	84	87	—	13	Surface section
6	7	356	84	—	16	,, ,,
7	7	106	81	—	19	,, ,,
8	7½	232	85	—	15	,, ,,
9	7½	146	77	—	23	,, ,,
10	8	186	83	—	17	,, ,,
11	8	192	81	—	19	,, ,,
12	8	152	81	—	19	,, ,,
13	9½	259	43	—	57	,, ,,
14	10	647	84	—	16	,, ,,
15	11	500	37	—	63	,, ,,
16	12	418	41	—	59	,, ,,
17	13	329	22	—	78	,, ,,
18	17	110	91	9	0	Scraping
19	18	279	93·5	6·5	0	,,
20	20½	296	7	12	81	,,
21	21	116	Some	14	—	,,
22	22	38	55	9	36	,,
23	23	53	79	9	12	,,
24	23	124	36	11	53	,,
25	24	375	22	17	61	,,
26	25?	159	20	18	62	,,
27	26½	247	21	13	66	,,
28	28	166	40	9	51	,,

Explanation of Table III.

a. Cultures were kept in an incubator at 22° C. and therefore conidia were formed at that temperature.

b. To bring about germination the conidia were transferred to fresh tap water (12° C.) and kept at bench temperature (16°–20° C.).

c. Two methods were employed of obtaining conidia for germination purposes: (*a*) the agar was scraped, (*b*) a surface section was cut. The objection to the former method is that younger conidia fall off their hyphal stalks more readily than older ones, which explains the high percentage production of zoospores in the cultures 18–28 days old.

d. Except in the second and third cases cited the age of the oldest conidia may be taken as three or four days less than the age of the culture; but in these two no conidia appeared on the culture until the eighth day, *i.e.* on the nine-day old culture the oldest were one day and on the ten-day old culture the oldest were two days old.

e. Nos. 1, 4 and 18–28 were cultures on potato agar, the others were on bean agar.

f. Percentage germination by tubes means that this percentage was found (when the culture was examined) to have already formed a germ tube. The cultures were not left long enough to see whether any more germinated after transference to water, as it was assumed that all the remaining ones would eventually give tubes.

g. The time elapsing before release of zoospores varied from seven to twenty-six minutes, being usually seventeen or eighteen minutes. The cultures were left for sufficient time to ensure that all likely to produce zoospores had done so.

method of germination. It will be seen that conidia (= sporangia) of young cultures germinate more readily by zoospores, whereas those found in old cultures germinate by a tube.

We have made further observations on *P. Colocasiae* and have found that if the culture was eight to ten days old most of the conidia became sporangia and emptied themselves of zoospores in ten minutes; if the culture was eleven to twelve days old, one or two conidia germinated by tubes and the rest took one hour to give zoospores. Thus we have confirmed Uppal's observations. The experiments already mentioned on submerged cultures of *P. palmivora*, might be recalled here (see p. 299). Similarly if cultures of *P. Fagi* were submerged for five days the conidia germinated by tubes. In such a stale medium fewer and fewer conidia are produced and these are less inclined to emit zoospores. The cause of this loss of power to produce zoospores may be attributed either to shortage of oxygen or to accumulation of staling products, both of which factors are frequent accompaniments of age, by which we mean a slowing down of metabolic processes. Such observations suggest that there may be a difference between the germination of a young conidium from a newly inoculated culture, *i.e.* from a hypha growing on a fresh medium, and a young conidium from an old culture, *i.e.* produced from a hypha on a staling medium. This is not necessarily proved by Table III where the older cultures were still producing zoospores from newly formed conidia, but it is suggested by the experiments with submerged cultures and also by Table IV, where it will be seen that on the whole a longer time must elapse between the addition of water and emission of zoospores when the cultures are older.

Table IV.

Age of culture (days)	Time between addition of water and emission of zoospores from the first conidium to germinate (minutes)	Age of culture (days)	Time between addition of water and emission of zoospores from the first conidium to germinate (minutes)
7½	11	13	17
8	8–9	17–18	14½
9	7	22	22
9	13	23	17½
10	8½	23	17½
10	12	24	17½
11	7	26–27	18
12	18	28	26
12	28		

Whereas it is easy to know the age of a culture, it is not easy to know the age of a conidium unless it has been kept under continual observation, for there is no apparent difference be-

tween a "sporangium" and a young conidium, and at one stage it does certainly appear that temperature alone may determine the method by which the spore shall germinate.

Resting conidia. Germination of resting conidia also may be induced by addition of water, sometimes supplied by condensation on removal of the containing vessel to a cooler atmosphere, or perhaps it may occur spontaneously.

But it seems that a conidium that has not germinated in the first week or two after formation sets up processes of maturation that involve a deposition of reserves on the innermost wall and an accumulation of fatty reserves in a large vacuole and that a certain time must elapse before germination of this altered body is possible. Murphy (1922) reported that conidia of *P. infestans* eight months old gave germ tubes only. We have found resting conidia of *P. Cactorum* at any age from six months to one year germinating by a tube, but as a rule in old cultures it is secondary and tertiary conidia of the chain that germinate, and it may be that within five or six months a resting conidium needs must germinate if only to produce immediately a new and smaller conidium. Some of these resting conidia on germination in water will give a short tube, and oogonia and antheridia at once (Text-fig. 5). For the production of resting conidia it is essential that the medium be kept continuously moist, especially while they are in process of maturation: complete desiccation means destruction. It seems clear that the stage of maturation reached determines not only the fact of germination but also the type of germination.

Chlamydospores. Chlamydospores were reported by Butler (1913) for *P. Colocasiae* and in the same year Dastur described them for the new species *P. parasitica*, saying that: "If kept moist they retain their vitality for over nine months, but if they are completely dried, their germinating power does not last for even a week." Rosenbaum (1917) described chlamydospores in *P. Faberi*, *P. Jatrophae*, *P. parasitica* and *P. Nicotianae*, and states that: "It is significant that in all forms which produced an abundance of chlamydospores no oospores were produced in the cultures," but this has since been disproved. He failed to obtain satisfactory germination of chlamydospores taken from young or old cultures.

We have successfully germinated chlamydospores of *P. parasitica* a year old (Text-fig. 7 A). These were found in an old tube culture that had been kept continuously moist at a temperature of about 15° C. They germinated readily on addition of water at 23° C. Gadd (1924) said that chlamydospores of *P. Faberi* from "old though still moist cultures" germinate readily. Ashby (1920) and Reinking (1923) observed germina-

tion of chlamydospores of *P. palmivora* within twenty-four hours.

It appears then that these chlamydospores undergo all the phases passed through by the resting conidia of *P. Cactorum*, and that the stage of maturation is an important factor in determining the method of germination.

Oospores. The germination of oospores has rarely been reported. Dastur (1913) stated that "resting conidia" (*i.e.* chlamydospores) of *P. parasitica* germinate readily when sown in water as compared with oospores which he could not make germinate. Pethybridge (1914) seems to have been the first to find germinating oospores, in a culture of *P. erythroseptica* nine months old. The germ tube produced a conidium quite soon. Rosenbaum (1917) sought for germinating oospores in cultures up to one year old without success until he hit on the idea of burying infected tissue for about six months. After this he germinated oospores of *P. Cactorum* and *P. Fagi*. Lafferty and Pethybridge (1922) obtained one germinated oospore of *P. Syringae* which gave a sporangium that liberated zoospores.

Rose (1924) says that "Germinating oospores have been observed a few times in old cultures on oat meal agar." We have quite frequently found oospores of *P. Cactorum* germinating *in situ* in cultures on Quaker-oat agar from six to twelve months old that have been kept continuously moist at a temperature of 23° C., although we have so far completely failed to induce germination of oospores younger than this. No doubt the explanation of Rosenbaum's success in germinating oospores five or six months old after sealing up the culture with paraffin wax, covering with a rubber cap, and burying deep in sand, is that by this means he kept the culture continuously moist.

The main factor in germination of oospores is clearly maturation. We have supplied different conditions of moisture, air and temperature, and have tried various media including extractions of the host plant but no germination has been obtained unless the oospore is ripe. At maturity the oospores germinate easily *in situ* even among the staling products of the mycelium which bore them.

Discussion.

From the foregoing summary of spores and spore germination it would appear that there is no precise distinction that can be drawn between sporangia, conidia, chlamydospores and sphaeroconidia in the genus *Phytophthora*.

Sporangia very soon become conidia, when they cannot be induced to give zoospores; and there is a transition stage where a drop of cold water will, after a rather longer interval than

usual, cause the sporangium to liberate zoospores (Table IV), or on the other hand a supply of water at a higher temperature will bring about direct germination. Zoospores induced to form in this manner usually escape by pushing aside the hardening papilla which cannot at this stage be expanded into a vesicle (Text-fig. 2).

Conidia ripen to resting conidia.

Chlamydospores appear to take the place of resting conidia in some species. Is it possible that temperate species produce resting conidia, tropical and subtropical species chlamydospores? The difference between them cannot be sharply defined: chlamydospores are usually without a papilla, are more nearly spherical in shape, have thicker walls, can remain viable longer and at a higher temperature. But the one does not develop into the other. Dastur (1913) says of the "resting conidia" of *P. parasitica* that "the thickening of the wall begins at a very early stage." Ashby (1929), describing chlamydospores of *P. palmivora*, says that "In old cultures, especially in those grown at high temperatures, the walls were often thickened and coloured." Gadd (1924) working on *P. Faberi* (= *P. palmivora*) reported zoospores inside some young chlamydospores; also empty chlamydospores which evidently had liberated zoospores. Sometimes he found a papilla present, sometimes a germ spore in the wall: in fact he reported spherical bodies with a papilla which produced zoospores when young and tubes when older. He regards chlamydospores as modified conidia as he found intermediate forms. In *P. parasitica* we have found every stage between a terminal or intercalary obpyriform sporangium and a terminal or intercalary spherical chlamydospore. Another observation made by Gadd concerns the variation in size and shape of conidia and chlamydospores in *P. Faberi*. He gives graphs which show that size varies with external conditions but that the shape is constant for the strain; also that those strains with wider sporangia show a greater tendency to produce chlamydospores, and that the variation in width of chlamydospores in the different strains corresponds closely to the variation in width of sporangia.

Leonian (1925) working on a number of species and varieties obtained from fifty-three sources stated that size and shape of sporangia vary much within each species. And again in 1926, working on rhubarb varieties of *P. Rhei*, he claims that among other characters the shape and size of the sporangia vary and that therefore these characters should not be used in taxonomy. Curzi (1927), reporting on a new species *P. hydrophila*, says that sporangia developed in water are obpyriform and that sporangia developed in air are lemon-shaped. Ashby (1929) criticises

biometrical methods of recording variation in size and shape of asexual reproductive bodies, but claims that on standard media under comparable conditions they retain a shape and size characteristic of the strain. It is of interest to note that Ashby recognises the influence of age of culture upon size and shape of sporangia of *P. palmivora*.

Thus shape and size are not strict criteria of type of spore. Nor is method of germination a criterion: the method of germination by zoospores leads by easy stages to that of germination by a tube; and resting conidia may give a germ tube through a germ pore (Text-fig. 5) as chlamydospores do. There is no evidence that conidia produced under certain specified conditions can be relied on to germinate by any given method.

Sphaero-conidia would appear sometimes to be nothing more than abnormal hyphal swellings in old cultures, which may be cut off by walls. *P. cryptogea* shows peculiar hyphal swellings of all shapes and sizes some of which might be considered to be sphaero-conidia. Sometimes they appear to be abnormal intercalary conidia: they give out germ tubes at any point which may or may not produce sporangia. Lafferty and Pethybridge (1922) figure and make reference to a sphaero-conidium which has a papilla.

Although chlamydospores germinating after a rest of nine months or a year look so much like germinating Oospores, there is always the old oogonium wall with the antheridium attached (or the oogonium wall alone in parthenogenetic oospores) to distinguish them.

In conclusion we would stress the importance of maturation in determining germination and type of germination. That there is an orderly sequence of events in the life of the fungus must be admitted. Spores cannot be produced, ripened and germinated altogether at will, *i.e.* by the application of selected external factors. There are still more important internal factors at work. But once the fungus is of an age and in a state to produce spores, production can be hastened or postponed; and once the spore is initiated and the maturation processes have set in, these can be accelerated or retarded by external factors, such as, *e.g.* temperature. Murphy (1922) realised this when, after careful cross experiments on germination of sporangia in different liquids at different temperatures (which revealed the fact that a lower temperature favoured zoospore formation and a higher temperature germination by tubes), he admitted that the "tendency to produce tubes is in the conidia themselves."

This of course only shelves the problem. It still remains to find out what is this orderly sequence of metabolic change that we call maturation. We know that water is necessary. The key-

note to successful production of ripe resting conidia, chlamydospores and oospores is the same: a long period of development on a slowly drying medium. All workers are agreed also that in a desiccated medium the spores do not mature but die. Oxygen supply and temperature are factors to be considered. There are changes in the nature of the reserves in spores of *Phytophthora*, leading to the accumulation of a large oily vacuole and the production of a thick cellulose layer on the inner face of the wall. Melhus has suggested that maturation involves changes in osmotic pressure.

That the state of maturation is the prime factor controlling germination is theoretically evident: the young spore has food and energy within it in an easily and quickly available form; the old spore has stores of reserve food laid down in a non-available and usually insoluble form and time must elapse before enzyme action can transform these into a soluble state, although this process may proceed quickly when once initiated. It is true that for this reaction a suitable temperature is necessary, and as Melhus (1915) says: "The time required for germination varies with the temperature," but the supplying of the optimum temperature cannot quicken the germination except through the maturation processes. Oxygen too is necessary for enzyme action. Once the reserves are in a soluble state the osmotic strength of the cell sap is raised and water is drawn in through the now thin wall (the thick reserve layer having been changed along with the other reserves) and the pressure exerted within ruptures the wall at its weakest point, or points, and germination takes place.

Under normal conditions then the determining factor in method and time of germination is the age of the spore.

Summary.

1. *Spores.* It is claimed that no sharp distinction can be drawn between "sporangia," "conidia," "resting conidia" and "chlamydospores" in the genus *Phytophthora*.

2. *Spore germination.* It is claimed that method of germination is dependent primarily on the particular state of maturation of the spore.

[For list of references see p. 320.]

THE PRODUCTION OF CONIDIA IN THE GENUS PHYTOPHTHORA.

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THE object of the investigation was to examine the influence of various conditions on the production of conidia in the genus *Phytophthora*. The species investigated were:

P. Cactorum, *P. cryptogea*, *P. Fagi* — Temperate.

P. Colocasiae, *P. palmivora* (= *P. Faberi*), *P. parasitica* — Tropical.

MATERIAL. Cultures on potato agar, ground Quaker-oat agar, bean juice agar and Knop agar were kept in both Petri dishes and test tubes, and temporary cultures in water were made as follows: small squares of agar infected with the mycelium were removed from slopes or plates with a sterile scalpel and transferred to tap or distilled water in watch glasses or small specimen tubes.

METHOD. In some cases the conidia were counted to determine exactly the actual increase during the period of the experiment, and for this purpose cultures on bean agar were used exclusively as this medium is more transparent than Quaker-oat or potato agar. A surface section was taken with a razor and the conidia were counted *in situ* by means of a squared micrometer eyepiece. Very few conidia fell off during the operation, so that a fairly accurate count was obtained and the number per square millimetre could be calculated.

The cultures were kept either in an incubator at 22° C., or on the laboratory bench at 15°–20° C., and the following conditions were investigated: (*a*) medium, (*b*) water, (*c*) air, (*d*) light, (*e*) temperature, (*f*) age of culture.

(*a*) *Medium*. The nature of the medium on which the fungus is growing affects the conidial production to a considerable extent. Most of the species of *Phytophthora* hitherto examined have been found to grow quite well in culture on solid media, as parasites on living tissue, or as facultative saprophytes on bean, oat, potato and corn agar; and to produce conidia to a greater or less extent. Exceptions however have been reported by Pethybridge (1913) in *P. erythroseptica*, and by Coleman (1910) in *P. Arecae*, where conidia were usually absent in culture. A similar lack of conidia in culture was found by Wormald (1919) in *P. Cactorum*, but later they were obtained quite readily

in this species by Rose (1924), by Rosenbaum (1917), and by other workers. They were also obtained abundantly during the present investigation. The most favourable medium for conidial production is different for each species but in general these reproductive organs are never so numerous on nutrient media as on the host plant or on living tissue. *P. Syringae* appears to be an exception to this rule, as Wilson (1914) stated that the conidia of this species are unknown in nature. A similar lack of conidia on the host was noticed by Pethybridge (1913) in *P. erythroseptica*, whereas they occur in watery extracts. Jones, Giddings and Lutman (1912), studying the effect of different kinds of media on *P. infestans*, showed that the fungus made a more favourable growth on a medium which gave a neutral reaction, and that it was more sensitive to an alkaline medium than to an acid one.

In the present investigation all the species except *P. cryptogea* produced conidia freely on the media used, cultures on bean and Knop agar giving them most abundantly. *P. cryptogea* did not form conidia on bean or Quaker-oat agar at 22° C. This is a result comparable to that obtained by Robinson (1915) investigating an unknown species on asters (probably *P. cryptogea*).

(*b*) *Water.* All workers have agreed that moist conditions are essential for the production of conidia. McAlpine (1910), for example, stated that he obtained conidia of *P. infestans* on potato tubers under moist conditions, and since that time various workers have made similar observations for other species. Vowinckel (1926) determined the actual moisture content necessary, and showed that unless there was a 73 per cent. saturation on the leaves or a 64 per cent. saturation on the tubers of a potato plant, no conidia of *P. infestans* would be produced.

Even if conidia are readily formed under these moist conditions, the presence of excess water materially increases their abundance. Thus Pethybridge and Lafferty (1919) found that if tissues infected with *P. cryptogea* "are allowed to stand in water many more spores are formed." Leonian (1925) requiring abundant conidia for examination grew his various species actually in water. This increased production is also evidenced in nature by the increased prevalence of the parasite during the more rainy periods, obviously due to an abundance of conidia, coupled no doubt with an easy production of zoospores. This has been described for *P. Phascoli* on bean pods by Clinton (1906), for *P. parasitica* on castor oil by Dastur (1913), and on rhubarb by Godfrey (1923), and by others.

Some species are so dependent upon moisture for the formation of conidia that they will not produce them until growing completely in water. Thus Pethybridge (1913) obtained abundant

conidia of *P. erythroseptica*, which were otherwise rare, in watery extracts of soils, and in rain water, to which a portion of infected agar or tuber had been added. In the same way Coleman (1910) obtained no conidia of *P. Arecae* in culture until portions were transferred to water, and Klebahn found the same treatment was required for *P. Syringae*. Robinson (1915) obtained the conidia of the species on asters by this method when other methods failed.

The results of this investigation are in accordance with those obtained by previous workers. Conidia of *P. Cactorum*, *P. palmivora*, *P. Colocasiae*, *P. parasitica* and *P. Fagi*, which are obtained readily on solid media, showed a considerable increase in numbers when the fungus was grown in water. Thus portions of an agar culture, where the mycelium was one day old and showed no conidia, produced them in abundance after twelve hours floating just on, or just under, the surface of the water. The numbers obtained by counting the conidia on portions in water, and on the controls on solid media, are shown in Table I.

Table I. *Cultures of* P. Cactorum *on bean agar at 22 ° C.*

Number of conidia per square millimetre		
At beginning of observations	After one night in water	After one night left on solid medium
1·5	4·0	1·75
0·0	9·3	4·9
0·48	26·5	13·5 (2 nights)
18·4	65·5	22·6 (2 nights)

Increased production in water was also shown by the number of conidia formed on each sympodium. Thus in *P. Fagi* there was an average of four to six conidia on conidiophores growing on solid media, and six to twelve on those growing in the water. Again with *P. Cactorum* there were never more than five conidia per conidiophore on solid media, but generally more in the water.

In accordance with the observations of other workers it was found that *P. cryptogea* did not produce conidia on solid media under normal conditions. Growth in water was therefore tried but the methods which had succeeded with other species gave no results here, periods of one, two and three days at 30° C., 22° C. and 16°–19° C., both in the light and in the dark being tried. Following an observation by Robinson (1915) that conidia of his species which closely resembled *P. cryptogea* were obtained after sixteen to twenty-one days in water, longer periods at 22° C. were tried, the water being changed periodically to keep down bacteria and to prevent accumulation of staling products. A few conidia appeared after fourteen days' immersion. One culture on Quaker-oat agar in water showed several after five days, and changing the culture to fresh water caused many

more to be produced after two more days. It is probable that conidia could be obtained after still shorter periods of immersion under more favourable conditions.

(*c*) *Air.* It has been generally observed from the time of de Bary that conidia are usually found on the surface of the host; the internal hyphae making their way out into the air before producing conidiophores. An exception to this was noted by Jones, Giddings and Lutman in 1912 who state that the conidia of *P. infestans* may be borne internally. Wormald (1919) showed experimentally that the conidia require air for their formation. He kept cultures of *P. Cactorum* in a closed vessel and conidial formation ceased. The only exceptional species appears to be *P. erythroseptica*, which was found by Pethybridge (1914) to produce conidia of an "essentially aquatic type," none being formed on aerial hyphae. It is assumed that oxygen is the necessary constituent of the air.

Definite experiments were carried out to ascertain whether the hyphae produce more conidia at the surface of the water than below it. Portions of agar cultures of *P. Fagi* were placed in tap water in small specimen tubes. Some portions were allowed to float on the surface, others were completely submerged. The cultures were kept on the bench.

Table II. *Production of conidia of* P. Fagi; *in cultures* (1) *floating on,* (2) *submerged in, water.*

Medium	Conditions	Time left	Floating	Submerged
Quaker-oat agar	Dark	1 day	Many conidia	Few
Bean juice agar	Light	1½ days	,, ,,	,,
,, ,,	Dark	2 ,,	13 per sq. mm.	11 sq. mm.
,, ,,	Light	2 ,,	42 per sq. mm.	0
Quaker-oat agar	,,	3 ,,	Abundant	Very few

Similar results were obtained with cultures of *P. Colocasiae*, where portions of agar were taken from the extreme edge of the radiating growth of the mycelium, which was consequently very young. Conidia were numerous on the floating portions after one night in water, but none appeared on the submerged even after five days. Again with *P. palmivora* at bench temperature the following results were obtained. After three days the floating portions bore twenty-seven conidia per square millimetre and there were six to eight on each conidiophore; the submerged portions bore twenty-five per square millimetre, with five to six on each conidiophore.

These experiments show that the conidial production is considerably reduced if the air supply is inadequate. If boiled water had been used instead of tap water, which contains some dissolved air, the numbers would probably have been reduced

still further, even perhaps resulting in the complete cessation of formation. All the results therefore point to the fact that air (*i.e.* oxygen) is a necessary factor for the formation of conidia.

The question, however, arises whether the non-production of conidia inside the host plant is really due to lack of air and whether the formation when the hyphae reach the exterior is due to its acquisition. The intercellular spaces in which the hyphae run are full of air and yet no conidia (except in one species) are formed there, not even the few that might be expected in a less adequate supply of air. Again the fact that the atmosphere of the leaf is moister than the air outside is another apparent contradiction of the conditions governing the process; but further consideration reveals the possibility that the surface film of moisture on the leaf is enough to cover the emerging hyphae. The important factor may therefore be the fresh water and not the air supply.

(*d*) *Light.* Previous investigations on light as a controlling factor in the production of conidia show rather varied results. Vowinckel (1926) working with *P. infestans* and Butler (1913) working with *P. Colocasiae* claim that light has no effect. On the other hand both Gadd (1924) and Reinking (1923) noticed that it had some influence on *P. Faberi*, Reinking finding fewer conidia in the dark. Coleman (1910) could obtain no conidia for five weeks in cultures of *P. Arecae* in darkness, but they were formed in two days in light. Dastur (1913) put forward the suggestion that alternating light and dark is essential for conidial production in *P. parasitica*: cultures kept always in the dark being sterile. It is of interest to note that in nature conidia are most frequently produced during the night and observed in the early morning.

The majority of the cultures used in the present investigation were kept in an incubator and were thus in more or less continuous darkness, except when the incubator was opened for the examination of the cultures. All the species formed conidia quite freely under these circumstances. Thus it appears that for the species examined full daylight is not essential for the actual formation of these reproductive organs, although it may have some effect on the extent of the production. Experiments were therefore carried out to ascertain if light would increase or decrease the numbers. Portions of agar infected with *P. Fagi* were used and when placed in water produced abundant conidia both in the light and in the dark at room temperature. Counting showed that sometimes there were more in the light (forty-two per square millimetre) than in the dark (twelve per square millimetre), sometimes there were more in the dark (eleven per square millimetre) than in the light (none per square millimetre). The experiments were not extended to other species but it was

noticed that conidia were always quite numerous in the dark at 22° C. Though further experiments are desirable, it appears doubtful whether light can be considered as one of the essential factors in conidial formation, although sometimes it may have an effect on the relative abundance.

(*e*) *Temperature.* Temperature affects conidial production in the same way that it influences other physiological processes, by acting as a limiting factor. The limits beyond which no sporangia are produced are not the same in the different species, and the optimum temperatures are also different. But there are indications that species found in temperate regions, *e.g. P. infestans* and *P. Cactorum*, have lower optima than tropical ones, *e.g. P. Faberi* and *P. parasitica*. Thus the optimum temperature for conidial production in *P. infestans* was found to be 16°–18° C. (Jones, Giddings and Lutman (1912)), and these workers also noted that no spores were produced below 10° C. or above 23° C. The optimum obtained by Vowinckel (1926) was 19°–22° C., and by Melhus (1915) 22°–25° C., but McAlpine (1910) obtained conidia of this species under special conditions at 27° C. Rose (1924) showed the optimum for *P. Cactorum* to lie between 10° C. and 20° C., and Uppal (1926) used a temperature of 22°–23° C. for maximum production in *P. Colocasiae*.

With tropical species on the other hand the temperature requirements appear to be much greater. Reinking (1923) could obtain no conidia of *P. Faberi* below 20° C., the optimum lying between 27° C. and 30° C., and Tucker (1926) claimed that 27° C. was the optimum. Similarly Ashby (1929) found the optimum for *P. parasitica* to lie between 27° C. and 30° C. The fact that tropical species require a higher temperature for fructification is to be expected from a consideration of the natural conditions under which they grow and produce conidia.

No definite experiments have been carried out to ascertain the effect of temperature on conidial production, but during the investigation it was noticed that differences did exist in cultures kept at different temperatures. This effect was particularly noticeable in the case of *P. Fagi*. Cultures kept in the incubator at 22° C. showed no conidia after two weeks and it was thought that this species, like *P. erythroseptica* and *P. cryptogea*, did not produce them on solid media. Cultures eight days old were then kept on the bench as well as in the incubator; the first showed abundant conidia after three days, but those at the higher temperature were still sterile. This was not due to the fact that those on the bench were in the light because, as shown above, light has no effect on the production of conidia in this species. It was assumed that it was due to the lower temperature, and to confirm this the experiment was repeated with cultures in water.

Again it was found that very few conidia were formed at 22° C., whereas they were abundant at the lower temperature. It was interesting to note also that many more sexual organs were present at the higher temperature than at the lower.

In the other species there was not such a marked difference between the extent of conidial formation at the two temperatures, but there was a certain retardation in growth at the lower; the fungus took longer to produce conidia, although after this longer period they were as abundant as at the higher temperature. Transference of cultures to the bench probably caused a slowing down of the metabolic processes and a consequent increase in the time that must elapse before conidial production. This retardation is shown distinctly by measurements of radial growth at the two temperatures. Thus the extent of the mycelium of cultures of *P. Cactorum* on potato agar plates at 22° C. is 3·25–3·6 cm. after seven days; whereas at bench temperature the time taken for the same radial growth is eleven to twelve days.

(*f*) *Age of culture.* The length of time which elapses between the inoculation of the medium and the appearance of the first conidium varies considerably with the conditions. Under optimum conditions this period is reduced to a minimum, but no one so far has been able to state the precise nature of such conditions. The shortest periods recorded, however, may be taken as most nearly reaching that standard. These are set out in Table III.

Table III.

Author	Species	Time elapsing before conidial production
McAlpine (1910)	*P. infestans*	7 hours
Hotson & Hartge (1923)	*P. mexicana*	48 hours
Ashby (1929)	*P. parasitica* var. *nicotiana*	1–2 days
Hopkins (1925)	*P. parasitica* var. on cotton	24 hours
Gadd (1924)	*P. Faberi*	2 days
Robinson (1915)	(*P. cryptogea*?)	16–21 days

It is possible that some of these periods could have been reduced by different conditions.

The periods noted in the present investigations with cultures growing under as nearly optimum conditions as possible were:

Table IV.

Species	Time elapsing before conidial production
P. parasitica	1 day
P. Colocasiae	1 ,,
P. palmivora	1 ,,
P. Cactorum	3½ days
P. Fagi	1–2 ,,
P. cryptogea	5 ,,

It has been noticed that the period is not the same for different parts of the same culture, even when these are approximately the same age. For instance in an agar culture in a Petri dish the outer parts of the radiating growth of the mycelium seem to lag behind the central parts in the production of conidia. This was confirmed by counting the conidia in different parts. The dishes were ringed after each day's growth, so that the age of any portion of the culture could be ascertained. The rings were numbered from the centre outwards and the conidia were counted on the portions where the rings were the same age. The counts are recorded in Table V.

Table V.

Age of mycelium (days)	Position in dish	Conidia per sq. mm.
4½	Ring 1	1·5
4½	,, 3	1·6
7	,, 2	22·6
7	,, 4	14·4
7	,, 2	53
7	,, 4	24
8	,, 1	60
8	,, 2	22
8	,, 3	18
12	,, 1	107
12	,, 2	82
12	,, 3	53
12	,, 4	18
24	,, 3	196
24	,, 4	53

Presumably all the parts of the plate were under the same conditions of medium, temperature, humidity, light and air supply, and yet there is a considerable difference in the abundance of the conidia. This suggests that there is another factor or factors, influencing the production of conidia besides those already considered. The effect may be due to the more congested state of the mycelium at the centre, the part at the edge being more spread out and in this region still expending material in establishing itself on the medium. The fact that there are more conidia at the centre than at the outside does not admit the possibility that the accumulation of staling products, if occurring, is having much inhibitory effect, as is sometimes found in plate cultures.

Conclusion.

Many factors apparently affect conidial production to a greater or lesser extent. Temperature and moisture content are the most important and act as limiting factors, temperature preventing the formation both at the upper and lower limits, and water at the lower limit only, for apparently no amount of water

is great enough to check the growth. The medium also is important, the fungus showing a more favourable growth in certain nutrient cultures. It is not clear which constituents of the medium cause the greatest abundance of conidia, although it has been shown that the relative acidity or alkalinity has some effect. It is probable that the moisture content of an agar culture is important here, since a moister medium like bean juice agar gives more conidia than a slightly drier one like Quaker-oat agar. The fact that the fungus produces conidia more readily on living tissue, which always has a high water content, is in accordance with this suggestion. Air is necessary to a certain extent and its absence may sometimes limit the process but conidia can be produced even when the air supply is very limited. The action of light and darkness on the formation shows varied results, but usually it appears that light is not a limiting factor; but whether it can modify the production at all, and to what extent, requires further investigation.

The combined effect of these conditions does not explain completely the story of conidial production. Certain results are not apparently due to the action of any of them, and point to the possibility of other factors also at work. Among these might be included the state of maturation of the fungus and the density of mycelial branching and growth.

In conclusion I should like to thank Miss E. M. Blackwell, M.Sc., Botany Department, Royal Holloway College, at whose suggestion the investigation was started, for her helpful advice and criticism throughout.

Summary.

1. The effect of certain conditions on the conidial production in species of *Phytophthora* has been examined.

2. Temperature, humidity, and air supply act as limiting factors, the two latter stopping the process at the lower limit only. The presence of excess water more than doubles the number of conidia.

3. The nature of the medium regulates the production, its action probably depending on its moisture content.

4. The precise effect of light is still doubtful; its presence or absence does not appear to cause any great variation in some species.

5. The time elapsing after inoculation and before conidia are formed, *i.e.* the age of the culture, is influenced considerably by the above conditions.

6. The number of conidia per unit area depends on the density of mycelial branching.

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OBSERVATIONS ON CERTAIN ASCOBOLACEAE.

By Ethel Green, M.Sc.

(With 7 Text-figures.)

Ascobolus stercorarius (Bull.) Schroet.

In 1924, cultures of *Ascobolus stercorarius* were made with a view to an investigation of the effect of artificial conditions of growth on the development and cytology of this species. The methods of culture, however, proved of sufficient interest to merit specialised study and this was extended to other members of the family. Since such a research must necessarily be prolonged, it seems worth while to make available the results already obtained, even though the work is still incomplete.

Since May, 1924, cultures of various specimens of *A. stercorarius* found on cow, horse, and rabbit dung have been made and maintained for periods varying from a few weeks to nearly four years.

In the earlier cultures the fungus was grown on decoctions of dung with 3 per cent. agar, and in the course of time invariably became sterile. As the constituents of dung are naturally variable it is almost inevitable that, sooner or later, a decoction will be

used that will be unfavourable to the fungus. From December, 1926, to the time of writing, material has been successfully subcultured on the medium *M* (2) containing:

0·1 per cent. magnesium sulphate,
0·1 per cent. tripotassium phosphate,
3 per cent. agar-agar,
0·1 per cent. ammonium nitrate,
0·01 per cent. sodium carbonate,
0·25 per cent. (approximately) filter paper.

In all cultures and on all media, numerous oidia (Fig. 1) were formed by the separation of the rectangular cells of the aerial

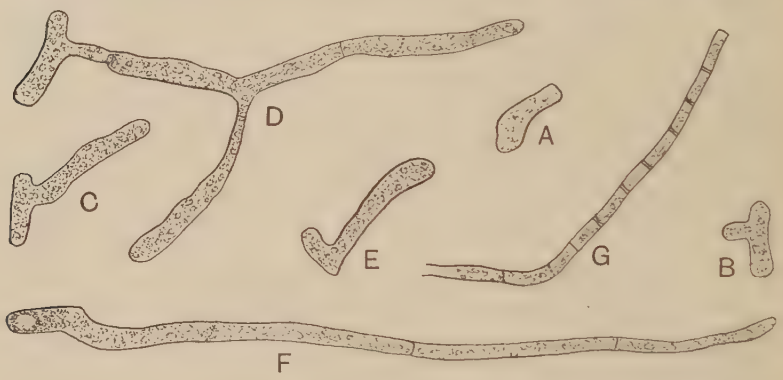

Fig. 1. A–F. Germinating oidia of *A. stercorarius*. G. Abstriction of oidia from aerial hyphae. × 800 approx.

hyphae, and were particularly abundant on mycelia failing to produce apothecia. They were first observed in 1924, when some were transferred on a cover slip to a plate of cow dung agar and left in the laboratory at a temperature of about 15° C. In eleven days many mature apothecia formed round the edge of the cover slip (Fig. 2) and subsequently others developed towards the periphery of the dish.

From the same material a culture was prepared from a single oidium. Small brown bodies resembling abortive apothecia appeared in this culture, and in a subculture from it, but fertile apothecia were not developed.

Earlier investigators (1, 4, 7) obtained germinations of the ascospores of this fungus after preliminary treatment such as incubation or digestion. Some of the ascospores used in these investigations have germinated after a variable period of incubation at 38°–40° C., but all preliminary treatment proved to be unnecessary, for germinations occurred spontaneously at a

laboratory temperature of 22° C. on the lids of the Petri dishes containing apothecia (Fig. 3). A resting period is not essential, for spores six days old have germinated readily.

Fig. 2. Mature apothecia of *A. stercorarius* formed at the edge of the cover slip.

Cultures of single ascospores have been made, some by the dry point, and others by the capillary method. Of twenty-three such cultures, seven have produced apothecia within periods

varying from one to nine months. The history of these seven spores is summarised in Table I.

Table I.

Single ascospore	Age of spore when sown	Time of germination	Time of fruiting	Initial culture medium
1	23 days	Within 30 days	Sterile brown bodies at end of 42 days	*M*
			When subcultured a large sterile apothecium was formed in 160 days	*M*, half strength, with 0·05 % calcium biphosphate and 0·025 % iron persulphate
			Many large mature apothecia in 276 days on subculture.	*M*
			These apothecia, subcultured, gave fruits in 10 days	*M*
3	10 days	Within 10 days	Many small fruits in 70 days; dried up without maturing. In subculture, good apothecia appeared in 290 days	*M*
4	21 days	Within 10 days	261 days	*M*
6	9 days	Within 10 days	185 days	*M*
7	45 days	6 days	212 days	*M*, incubated 1 hour at 49° C.
14	36 days	?	28 days. Fruited in 14 days in subculture	*M*
19	36 days	?	35 days	*M*

Fig. 3. Germinating ascospores of *A. stercorarius*. × 800 approx.

Petri dishes were inoculated on opposite sides with mycelia from single ascospores. In some of these, apothecia were formed across the line of mycelial junction or were distributed irregularly over the dish: in others, no apothecia were produced. When these experiments were carried out, ascospore 7 had produced no fructifications by itself but had fruited vigorously with ascospore 2. These two spores were therefore considered to be of complementary types, *A* and *B*, and were used to test the types of the other single spore cultures. Of the twenty-two monosporic cultures tested, twelve, *A*, fruited with the mycelium from ascospore 2, and eight, *B*, gave no apothecia with this strain but fruited with the mycelium from ascospore 7. The seven single ascospore cultures which produced apothecia alone, fall into group *A*, for up to the time of writing they have, with a single exception (Table II, ascospore 6), failed to fruit with *A* mycelia, whereas with mycelia of group *B*, they fruit much more rapidly than alone†.

Table II.

No. of ascospore	1	3	4	6	7	11	5	9	2	8	10	Time of fruiting of single spore
1	—	—	—	—	—	—	—	—	10	25	32	276
3	—		—	—	—	—	—	—	24	13	25	70
4	—	—		—	—	—	—	—	13	14	38	261
6	—	—	—		—	—	89*	—	14 on *M*	19	25	185
7	—	—	—	—		—	—	—	17	25	25	212
11	—	—	—	—	—		—	—	13	13	13	—
5	—	—	—	89*	—	—		—	86–115	28	—	—
9	—	—	—	—	—	—	—		18	19	—	—
2	10	24	13	7 on *M* with dextrose	17	13	86–115	18		—	—	—
8	25	13	14	19	25	13	28	19	—		—	—
10	32	25	38	25	25	13	—	—	—	—		—

The numbers in the columns indicate the time of fruiting (in days).

The results obtained by pairing mycelia from eleven single ascospores are shown in Table II. A — sign indicates that no apothecia were formed; the blank spaces show that the tests were not carried out with ascospores 3 and 9. This was due to the fact that the culture of ascospore 9 was inadvertently destroyed. The formation of apothecia by mycelia from ascospores 5 and 6, which are of the same type, may be due to the ability of the mycelium of ascospore 6 to fruit alone.

Table III shows the result of growing mycelia from ascospores 2 and 7, respectively, in juxtaposition with mycelia from twenty-three single ascospores. All fruiting with ascospore 2 are of type *A*; those fruiting with ascospore 7 are of type *B*.

† Ames, L. M., in "A study of some homothallic and some heterothallic Ascomycetes," *Mycologia*, XXIX (1930), pp. 318–322, describes such mycelia as hetero-homothallic.

Table III. *Table showing the results obtained by growing mycelia of single spores with mycelia of spore 2 (type B) and with spore 7 (type A).*

No. of spore	1	2	3	4	5	6	7	8	9	10	11	12
2	+	−	+	+	+	+	+	−	+	−	+	−
7	−	+	−	−	−	−	−	+	−	+	−	−

No. of spore	13	14	15	16	17	18	19	20	21	22	23
2	−	+	−	−	+	−	+	+	+	−	−
7	+	−	+	+	−	+	−	−	−	+	+

+ indicates the production of apothecia.

Fruits were also obtained when groups of oidia from complementary mycelia were sown in the same dish; but of eight cultures from single oidia, only one fruited, producing three small fertile apothecia.

Mycelia from a single ascospore of type *A*, and from a single oidium, isolated from a culture of an ascospore of type *B*, have fruited well together, but no result has so far been obtained when mycelia from cultures of single oidia from two complementary mycelia were grown in juxtaposition.

As most of the single ascospore cultures which fruited alone did not produce apothecia until after a comparatively long period, the possibility of contamination of the culture by oidia from a complementary strain was considered. A direct infection was made on a fairly old culture of ascospore 1 with oidia from mycelium of complementary type. No apothecia were formed. Moreover many hundred cultures of different fungi have been kept in the same laboratory close to the plates of *A. stercorarius* and none of these has ever been contaminated by the intrusion of *Ascobolus*. Thus the possibility of seven single ascospore cultures each being accidentally infected with a spore of complementary type may reasonably be disregarded.

It seemed possible that some connection might exist between the development of fruits and the *p*H of the medium. Tests with universal indicator, however, showed that when mycelia from different spores were growing on opposite sides of the Petri dish, there was no appreciable difference in the *p*H of the medium *M*. Seventeen non-fruiting pairs and five fruiting pairs were tested with the same result. In one case only was there a difference observed, the *p*H of the two sides being 8 and 7 respectively: a line of apothecia was formed across the middle of the dish.

On Claussen's medium in which starch was substituted for inulin, the mycelia grew very slowly, but eventually met and interpenetrated. Although with two exceptions no fruits were

formed, in all the line of junction remained distinct, as a clear translucent band visible until the culture had completely dried up. Fresh uninfected medium had a *p*H of approximately 5. Two plates infected, one with mycelium of a non-fruiting, and the other with the mycelium of a fruiting pair, were tested just before the hyphae had met. In both the *p*H of the medium on opposite sides of the plates ranged from 4–5, while that between the tips of the hyphae ranged from 6·5–7.

On this medium, two cultures were prepared of the same complementary mycelia. One of them fruited in sixty-three days: the other was contaminated by a Hyphomycete and fruited in twenty-five days. Normally, since the medium contains 1·5 per cent. starch, the addition of iodine produces a deep coloration. This did not appear when iodine was added to the contaminated medium, indicating a change in the substratum which renders the starch easier for the *Ascobolus* to assimilate. The same complementary pair of mycelia fruited in twenty-eight days on the medium *M*.

Five spores from the same ascus, grown on one plate, produced apothecia, but up to the time of writing, attempts to separate the eight spores of an ascus have failed. In some asci the full number of spores does not develop, so that often only five, six or seven mature spores are formed.

Within the strict meaning of the word, the mycelia from ascospores of *A. stercorarius* which have been tested during this investigation may be regarded as heterothallic, for they fall into two groups producing apothecia where their mycelia are in contact. Possibly the staling products of either strain alone inhibit fruiting, or either alone is unable to accumulate from the medium the necessary food materials, except in certain members of group *A*. In the former the effect of staling products is presumably overcome by the complementary mycelia; in the latter, mycelial fusions may be expected, as observed in *Coprobia granulata* (3). Even in monothallic cultures numerous fusions occur, but the relation of mycelial fusions to the production of apothecia has not been studied.

Ascobolus glaber Pers.

In 1926 this fungus was found on rabbit dung, and was grown on rabbit dung agar. It was subcultured both from mycelia and from apothecia and fruited well for three months. At the end of that time it became sterile, but, four months later, when strands of mycelium were laid on moist pellets of rabbit dung, apothecia were formed and cultures from them were maintained for nearly two years. When they once more ceased to fruit they were allowed to lapse. Other cultures, also, of *A. glaber* from

different sources rapidly became sterile and, to maintain fruiting specimens, frequent subcultures are essential.

The ascospores of *A. glaber* very closely resemble those of *A. stercorarius*. They were shot on to the lid of the Petri dish and germinated twelve days later at laboratory temperatures varying from 18°–22° C. (5). Spores shed on the agar germinated in four days and fruited within thirty-five days of their liberation. The germ tubes arise laterally or terminally and may branch immediately after their emergence. Fusions between hyphae of different spores have occasionally been observed (Fig. 4).

Fig. 4. Germinating ascospores of *A. glaber*. × 800 approx.

Germination takes place readily at all times of the year, nor is a period of rest important, since spores shed in January germinated with equal readiness after four, and after three hundred and seventeen days.

A. glaber produces oidia which resemble those of *A. stercorarius* both in appearance and behaviour; the archicarps also are very similar (Fig. 5).

Dasyobolus immersus (Pers.) Sacc.

Apothecia found on horse dung in May, 1927, were transferred to rabbit dung agar. In twelve days fruits appeared and the fungus was subcultured successfully for a year. It then became

sterile and though subcultured for some months, failed to produce apothecia.

Subsequently four inoculations with single ascospores, shot from apothecia on rabbit dung, were made on the medium *M*, and were left at a temperature of about 22° C. Of these spores, three germinated readily and the fourth after thirty-nine days. Fructifications were not formed, nor were six other monosporic cultures successful. From groups of spores apothecia were obtained in eleven or twelve days. It is hoped to deal further with the question of heterothallism in this species.

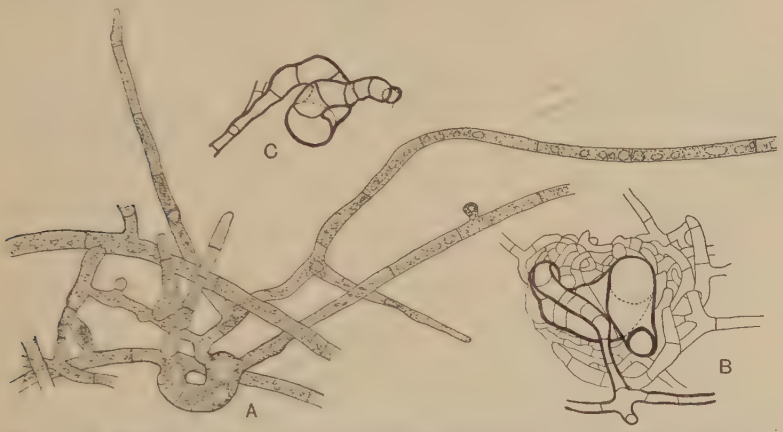

Fig. 5. A. Sterile archicarp of *A. stercorarius* continuing growth vegetatively. B. Young apothecium of *A. stercorarius*. C. Archicarp of *A. glaber* just before sheath formation. × 800 approx.

Saccobolus obscurus (Cooke) Phill.

This fungus, found growing on the dung of deer and of rabbit, was cultured on four occasions during 1926 on rabbit and on cow dung agar. In every case the fungus fruited well, but owing to the presence of impurities the cultures lapsed after a few months. On the synthetic medium *M* material was kept in culture for three years before becoming sterile.

Fruits were formed at all periods of the year at laboratory temperatures of 18°–22° C. and shot their spores on to the lids of the Petri dishes where they germinated without treatment. The spores are liberated in groups of eight, held closely together by mucilage (6). Occasionally separate spores have been seen, but all the germinations observed have been those of spores of a group (Fig. 6). No naturally isolated spore has been seen to germinate and, up to the present, no attempts to germinate artificially separated spores have been successful. Often the

spores seemed to need a resting period and most of the germinations occurred after a period of quiescence lasting from fifty to one hundred and thirty days. Two germinations took place in June and July in nineteen and twenty-one days respectively.

Cultures of groups of spores fruited in an average period of one hundred and twenty days after liberation from the ascus, the shortest time being eighty-two days, when fruits were formed in February, and the longest one hundred and forty-six days, in September.

Fig. 6. Groups of spores of *S. obscurus*. A, B. Two spores germinating. C. Only one germinating spore in the group. D. Group of eight germinating spores. Dotted outline indicates mucilaginous investment. × 800 approx.

Cultures made from mycelia usually take three weeks to fruit and the shortest time for fruiting has been fifteen days. During the last six months that the fungus was in culture the fruits were produced infrequently and were very much smaller.

The archicarps are small and usually become very much entangled and interwoven so that it is difficult to determine the number in an apothecium, but it seems as if any number from one to seven, or even more, may be enclosed in a common sheath which arises very early and grows very rapidly (Fig. 7). The cells of the very young archicarp are uninucleate, but become multi-

nucleate during the formation of the sheath. Apothecia are often sunken in the agar, and the orientation of the asci seems to be a matter of indifference. Frequently they are pressed against the bottom of the Petri dish pointing in the opposite direction from those at the free surface of the agar. Often double apothecia are formed, one member having its asci growing upwards into the air while those of the other grow directly downwards into the agar.

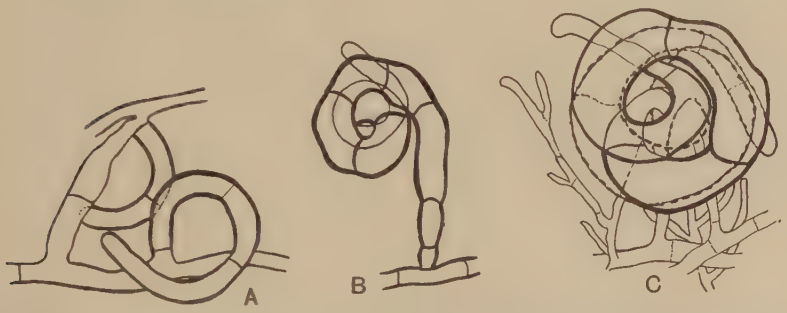

Fig. 7. Archicarps of *S. obscurus*. A. Two young archicarps. B. Archicarp just before sheath formation C. Two entwined archicarps with developing sheath. A, B, × 2000 approx.; C, × 3000 approx.

The best results were obtained when the fungus and the spores were allowed to grow at laboratory temperatures; mycelia incubated at 25° C. failed to produce fruits, and spores incubated at 40° C. did not germinate.

No accessory spores were observed in any of the cultures.

Summary.

1. Ascospores of *Ascobolus stercorarius*, *A. glaber*, *Dasyobolus immersus*, and of *Saccobolus obscurus* germinate at a temperature of about 22° C. without preliminary treatment.

2. Ascospores of *A. stercorarius* are of two types, *A* and *B*; apothecia are readily formed when mycelia from these are cultured in juxtaposition. A few monosporic mycelia, all of type *A*, have produced fertile apothecia, but usually after considerable delay.

3. *A. stercorarius* and *A. glaber* produce abundant oidia which germinate very readily, and are very similar in appearance and behaviour.

The research was carried out at Birkbeck College and I wish to thank Professor Dame Helen Gwynne-Vaughan for stimulating suggestions and criticisms. Thanks are due also to

Mrs H. S. Williamson, B.Sc., Miss W. M. Page, M.Sc., and Miss E. A. Potter, B.Sc., for specimens.

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STUDIES IN THE MORPHOLOGY OF DISCOMYCETES.

V. THE EVOLUTION OF THE ASCOCARP (*continued*).

By E. J. H. Corner, B.A.

It is contended that the existing kinds of Discomycete ascocarp are juvenile expressions of a multaxial soma which bore cupular apothecia. The origin of this hypothetical form will be examined in this paper, but firstly the current views on the evolution of Discomycetes will be considered. There are three main standpoints which cover generally the case of Ascomycetes, and it will be shown that the hypothesis of juvenescence is applicable also to the Pyrenomycete ascocarp.

In the first place it is held that there is a kingdom of Fungi distinct from those of Plant and Animal, though it may have originated from the simplest algae or protista. It is a kingdom of heterotrophic organism, saprophyte and parasite, characterised by the evolution of an absorptive mycelium and a sporogeneous fruit body, with an elaborate reproductive equipment, sexual and asexual. The unit of construction is the hypha, or heterotrophic filament with apical growth, which is believed by some to be the outcome of the chytrideaceous rhizoid (12). Biologically the kingdom shows an upgrade in the colonisation of subaerial environment from unicellular aquatic or simple multicellular Phycomycetes to complex Basidiomycetes. Ascomycetes are derived from Phycomycetes and Basidiomycetes from Asco-

mycetes though the way is not precisely certain. The Pyrenomycete and Discomycete ascocarps are derived from the plectascalean cleistocarp and, in contrast with the writer's hypothesis, the largest and most complex of these fructifications, as those of the Morchellaceae and the Xylariaceae, are held to be the most highly evolved. The standpoint follows naturally from the close resemblance between these groups of fungi in mode of life, in structure and reproduction. It apparently is based on the supposition that the first terrestrial fungi were simply organised in as much as it is held that there was only a simple lowly autotrophic vegetation for their subsistence. Some Ascomycetes, as the Hemiasci, certainly approach the Phycomycetes closely in the absence of any fruit body and in the simplicity of the sporangium, which nevertheless is recognisable as an ascus, and such forms lead by small gradations to the most complex. There is an almost complete morphological series from the naked ascus of *Endomyces* to the fruit bodies of *Morchella* and *Xylaria*. But the series can be read both ways and the contention that the simple forms of ascocarp are primitive does not rest on a detailed comparison of simple and complex forms within a small circle of affinity such as undoubtedly occur. I have attempted a comparison of this kind in the Operculeae and have found that there is no simple ascocarp in these fungi which cannot be related either on its own grounds or by analogy to the more elaborate ascocarp of some allied species or genus as a juvenile form derived by degeneration. At least in one large group of Ascomycetes therefore the simple forms are not primitive, and clearly the possibilities of reduction must be exhausted before that which is simple can be pronounced primitive, most especially when dealing with modern organisms. Reduction in one form or another is obligate with specialisation and the Hemiasci and Plectascales, being typically saprophytes in rich organic fluids or cutaneous parasites, are as specialised if not more so than *Pyronema*, *Thelebolus* or *Neotiella Crozalsiana*, which have been shown to owe their simplicity of ascocarp to the special conditions of its production. The ascocarps of these Discomycetes must be considered primitive on the upgrade theory and those of *Helvella* and *Morchella* among the latest products of evolution in the group, yet the environmental factors conditioning the development and function of ascocarps of *Helvella* and *Morchella* are much more general and less exacting. As a matter of fact the biological aspect of the upgrade theory has not been adequately discussed. Why, for instance, should large complex fruit bodies with a prolonged period of inactivity have been evolved? Why, if small ascocarps are primitive, should they be so common and widespread to-day and why so characteristic of

specialised, advanced habitats? And if the cleistocarp has evolved from the integumented Phycomycete zygote and the apothecium from the cleistocarp, in what way more likely than that which may be read in the series *Thelebolus—Rhyparobius—Ascophanus*? It is improbable, however, that an apothecium is being evolved to-day on cow dung in our farmyards. Yet if degeneration be admitted in this case as well as in that of *Neotiella Crozalsiana*, where can a line be drawn to separate the primitively simple from the reduced? Evidence is lacking, in my opinion, that any simple ascocarp belongs to a primitive fungus. The study of the somatic organisation of the ascocarp introduces a fresh set of facts and the conclusion to which they point is in agreement with that drawn from the study of the reproductive organisation, which is generally admitted, since both reveal degeneration. But still another matter must be explained before an upgrade of the ascocarp can be accepted. Why do all the kinds of Discomycete ascocarp conform to one plan, to the same developmental series? Greater diversity is surely to be expected in fungi which, it is claimed, have evolved the complexity of the Ascomycete from the insignificance of the Phycomycete. And why, on the upgrade theory, are intermediates so common even within the limits of a single species, as in *Rhyparobius*, *Humaria*, *Peziza*, *Acetabula* and others, as if the upgrade still continued? It is very unlikely that intermediates and primitive forms should have persisted to the present time. It is contrary to the principle of natural selection, and, if true, Ascomycetes show a state unlike that in any other class of complex organism where the disappearance of intermediate stages has naturally and exclusively defined the larger systematic groupings as genera and families. This is perhaps the weakest point in the upgrade theory and as the writer has tried to show it may be ascribed to the artificial classification of the group. Where natural series can be recognised as in the Operculeae, they are found each to contain parallel forms of ascocarp and this can readily be explained on the ground that the ascocarp has developed in each series by the same process from a similar ancestral state which can be traced nowadays certainly to the stipitate apothecium and when the nature of *Wynnea* is better known, in some cases perhaps to a multaxial form.

In the second place Ascomycetes have been related to Florideae on the grounds of a common life-cycle and reproductive organisation. Apothecium and perithecium are homologised with the cystocarp, and archicarp with procarp, while spermatogamy occurs in Laboulbeniales and some Lichens. The comparison cannot be pressed too closely for ascogenous hyphae and gonimoblasts appear to differ essentially in detail. The stand-

point does not reckon with somatic organisation. Only the smaller lenticular and turbinulate apothecia are considered in detail and there is explanation neither of the disappearance of the algal soma, as in *Ascobolus*, *Sphaeria* or *Eurotium*, nor of the evolution of the supposedly higher forms as *Morchella* and *Xylaria*. It is undecided whether apothecium, perithecium or cleistocarp represent the primitive kind of ascocarp (1, 8). But assuredly if the apothecium or perithecium is comparable with the cystocarp, then the axis of the ascocarp, or the stem region, is comparable with the axis of a red alga, since both are gametophytic and of similar construction. One is thus lead to the third standpoint which obviously is radical in that it deals with the origin of the somatic organisation of Ascomycetes.

Church (2) has approached the problem of the evolution of fungous fruit bodies from the standpoint of algology. "The beginnings of Botany are in the sea," and one must know what is there and how it came there before turning to the problems of land vegetation. Church emphasises the importance of this comprehensive botanical outlook and the value of somatic organisation as an index to phylogeny. The uniseriate algal filament and the hypha are morphologically equivalent: both consist of a branching row of nucleate cells of the same order of size, enclosed within a cell wall of polysaccharide matrix, and cut off from a special apical cell. The gametophytic portion of an ascocarp, *e.g.* the stalk and excipulum in *Helvella*, are morphologically equivalent to the cable type of algal soma, *e.g.* *Nemalion*, *Chordaria*: in each there is a medulla of longitudinal main filaments with interwoven, binding secondaries, and a palisade layer of cortical filaments perpendicular to the surface, in the manner of a condensed filamentous system, and in each the growing point consists of the juxtaposed apices of the main filament. Admittedly in the alga the cortex is photosynthetic on the outside, but the presence of the same factors of equipment, building the same kind of soma, in alga and fungus must be taken as an instance of homoplasy. Now homoplasy means independent and parallel evolution in response to the same causation. The somatic organisation of the Ascomycetes, therefore, must have been inherited from algae which had advanced to the level of the cable type of soma in marine benthic environment. It is a level that has been reached independently in the Phaeophyceae, Florideae and Codiaceae, and that it is a common property of plants with such different metabolism and protoplasmic mechanism shows that it is but an expression in each phylum of algae of the evolution of autotrophic organism following on attachment to the sea floor. Church concludes that the primary factors that have affected the evolution of

marine phytobenthos have been the demand for maximum surface exposure for absorption of light and food ions, and the need of fixation and mechanical strength of cohesion in the tissues to resist the force of the moving medium. On these lines Church has endeavoured to describe the causal evolution of the various kinds of algal soma which represent so many means of overcoming the problems of existence for multicellular plants in the different stations of benthic environment. It is obvious, that this granted for algology, a similar causation could not have occurred in subaerial environment, where desiccation is a primary factor unfelt by phytobenthos, and much less in connection with a heterotrophic organism which consists of a system of absorptive filaments immersed in the substratum and a fruit body which is fed from below and which tends to a minimum surface area in response to the loss of water. This fruit body in its most elaborate form consists of a cylindric axis with dichotomising frond systems, of the cable type, bearing numerous immersed gametophoric ramuli, exactly in the manner of a complex floridean; and yet it is subject neither to the demands of an absorptive assimilatory layer, nor to the tensile strain of moving water. It dwells in the forest base in quiet decay and that it is equipped in the same manner as an alga which has always lived in the sea and can stand the force of a breaking wave, can be explained only by concluding that the larger Ascomycetes are descended from large complex marine algae which migrated on to land. These algae became heterotrophic in subaerial environment and developed a system of absorbing filaments, perhaps foreshadowed in a preliminary filamentous phase, while the soma was retained solely for its reproductive function and has degenerated in a manner expedient with the new set of environmental factors.

Likewise Church accounts for the reproductive mechanism of Ascomycetes (4). It is to be explained as inherited from organisms which have passed through a planktonic stage or zoidogamy to the benthic stage of oogamy with fertilisation *in situ* and a diphasic life cycle with the meiotangium produced on the parasitic sporophyte. The coenocytic ascogonium represents the plurilocular oogonium, the coenocytic antheridium represents the plurilocular antheridium of the alga and the ascus is the meiotangium (5). Such mechanism has been evolved by autotrophic organisms which have never emerged from the sea and where it occurs in land organisms it must indicate an original phase of benthic evolution. The difficulty lies perhaps in recognising beyond doubt the organisation in the reduced degenerate form in which it occurs in modern fungi, but this aspect has been fully developed by Church and need not be considered further here; the main points are evident.

Now by Church's method the transmigrant algal state of a phylum of subaerial plants can be deduced in the main by the abstraction of the factors of equipment of marine phytobenthos from that phylum, since each factor represents a relation between autotrophic organism and marine benthic environment, and it is the largest and most complex members of the phylum, as *ex hypothesi* they are the least reduced, which will afford the nearest approach to the transmigrant state. This state for each of the three main series of Discomycetes, Pyrenomycetes and Lichen fungi will therefore be a multaxial cable type of gametophytic soma bearing numerous "ascocarps" which represent the compound post-sexual fructifications developed in connection with the parasitic sporophyte. Thus it follows that the primitive type of ascocarp was multaxial and polycarpic, which is the conclusion I have drawn from the study of existing Discomycetes. The original possession by Discomycetes of a cumbrous multaxial soma is thus explained as a legacy from a former phase of existence. Such a form is ill-adapted to modern requirements, being barely represented in the large group of Discomycetes, and the point is sufficient to show how different must have been the environmental conditions under which these fungi were evolved. It is necessary to attempt to visualise the nature of the hypothetical transmigrant algae and of their environment.

In the first place one naturally enquires if Ascomycetes are related to any existing algae and why they became heterotrophic on migration to the land. The loss of assimilatory pigments and of zoospores precludes the reference of Ascomycetes, like any other group of fungi, to a flagellate basis and thus to an algal series. The definitive characters of primary importance disappeared with the assumption of heterotrophy and mere agreement in the possession of the same factors of equipment in phytobenthos and its derivatives does not imply relationship owing to the essential element of homoplasy. Nevertheless it is remarkable, as Church has pointed out, that the hypothetical transmigrant forms deduced for living Ascomycetes should have so many features in common with Florideae and yet display an older, lower level of organisation. They seem to fill to some extent the necessary postulate of Prefloridеae, or algae antecedent to Florideae, that great isolated phylum of seaweeds. Ascomycete and floridean agree in the type of somatic organisation of the gametophyte, in a point of cell construction in the pitting of the crosswalls, in the general reproductive organisation with a parasitic filamentous diploid generation which, be it observed, is a unique property. But in respect of the diphasic life cycle and the meiotangium reduced only to an octad and, perhaps, the filamentous portion of the oogonial hypha distal to the fertile

part, as the "septate trichogyne," Ascomycetes are behindhand. It is enough to realise the resemblance and the possible significance of Ascomycetes in the reconstruction of the history of marine plants. The resemblance cannot be pressed too closely, for the "ascosporophyte" with hook mechanism in the diploid filaments seems to differ intrinsically from the carposporophyte; and how many algal series so equipped may not have flourished in primeval seas?

Church ascribes the loss of autotrophy to the novel conditions of the environment of transmigration and to the inferior metabolism and equipment of the algae in question. On the emergence of land vegetation for the first time plant remains accumulated where they fell and a new environment was opened at the base of autotrophic vegetation, among the incipient root systems, for inferior algae unable to cope with their betters in the struggle for photosynthetic position. That the transmigrant algae which, it is supposed, gave rise to Ascomycetes were of inferior calibre is shown by the fact that they had a gametophytic soma on which the sporophyte was decadent and which bears no trace of ever having reached the level of parenchymatous construction. No autotrophic plant without a massive parenchymatous free-living sporophyte has succeeded on land and the cable type of soma is mechanically inferior to the parenchymatous, which is a deficiency to be augmented on land where the plant must support its own weight. It is natural that such organisms should be exterminated in competition with better types, or avoid the struggle by assuming the new mode of life offered in the environment of transmigration. Moreover if Ascomycetes are related phylogenetically with Florideae, that may account for the inferior metabolism of their algal ancestors and detract in addition from their likelihood of success in competition with parenchymatous chlorophycean derivatives.

If the transmigrant Ascomycete possessed a large multaxial soma a foot or so high, at once a problem is raised how such a form ever managed to establish itself on land. If a primitive saprophytic organism possessed a soma of such dimensions, then a luxuriant autotrophic vegetation is implied for its support with equal problems of transmigration. If the hypothesis of juvenescence of the ascocarp is correct, it follows that the primitive land vegetation must have consisted in major part of massive autotrophic plants and that the land flora must have originated in the manner which Church has postulated. The implication, it might be expected, would condemn the hypothesis which the writer has proposed, inasmuch as the transmigration from sea to land of massive plants is as impossible to conceive as it is impossible of realisation nowadays. But who knows what the

world was like in precambrian times? The objection is illogical, founded on the supposition of an exceeding constancy of physical conditions in the development of the world. On the contrary, the facts in the case of Discomycetes, meagre though they are, appear to me so conclusive that the hypothesis may be regarded as a contribution from mycology to a common problem of botany rather than as self-condemning. The facts point to the degeneration of a complex soma and algology explains the presence of the original soma which degenerated: the combination is in itself sufficient to give the hypothesis of transmigration.

Thus the problem of the ascocarp becomes the metamorphosis of a complex algal soma into a heterotrophic fruit body, a mere reproductive organ. There is still evidence enough of the later stages of this evolution, but of the initial stages, as might be expected, there is no trace: they were enacted under conditions which no longer exist, and clearly this period of transmigration marks an epoch in the world's history if only because it introduced the fungi. Such a multaxial form as *Wynnea*, as Church points out, has probably never emerged from the humus layer which accumulated at the base of transmigrant vegetation and has accompanied it to the present time as a fungus of the forest base. On the other hand, relegation of inferior races into inferior and specialised habitats as they were crowded out in the struggle would have lead to the reduction and refinement of the original soma with its extravagant demand for sterile tissue, and so would have evolved the very efficient minute sessile ascocarps, the product of a single sexual act, which abound at the present time. They who maintain that these forms are primitive and that the largest, the most elaborate are the latest, have yet to explain the homoplasy between the algal soma and the fungous fruit body, and until it can be shown that a parallel evolution of heterotrophic organism in subaerial environment and of autotrophic organism in marine benthic environment can have taken place it seems that no other conclusion can be adopted than that which Church has already drawn.

Pyrenomycetes.

Church's hypothesis covers the case of Pyrenomycetes as well as of Discomycetes and a cursory examination shows the same to be true of the hypothesis of juvenescence. One would expect two similar groups of fungi to have evolved on similar lines and a brief account of the ascocarp of Pyrenomycetes will not be out of place.

A multaxial form of ascocarp is found in several genera, as *Xylaria* and *Thamnomyces*, where it may be flattened, dichotomous and with numerous perithecia borne distally like the

frond system of a red alga, *e.g. Chondrus crispus*. It is a more frequent form than in Discomycetes, perhaps on account of the xerophytic property of the carbonaceous surface and the immersed hymenium, and it is employed even by some of the commonest Pyrenomycetes. A reduction already appears in *Thamnomyces*, for each branch of the stroma bears only one perithecium (9). But the main reduction series can be traced in a variety of monopodial forms from the "stipitate" form of *Cordyceps* or *Claviceps*, through sessile, pulvinate, discoid and crustaceous forms as in *Hypoxylon*, *Diatrype*, and *Ustulina*, through the loose aggregation of perithecia on a mycelial subiculum, as in *Rosellinia*, to the local aggregation of individually distinct perithecia and the isolated perithecium which make up the host of *Sphaeria*. Parts of the series can be traced within small circles of affinity just as in the Operculeae. There are, for example, multaxial and monaxial forms in *Xylaria*, and *Valsa* and *Hypoxylon* have pulvinate and discoid stromata and more or less isolated perithecia, and the whole series may be traced in the allied genera *Xylaria-Hypoxylon-Rosellinia*. But the simple perithecium is not the end term of the series; there are several different forms of isolated perithecium which can also be interpreted as juvenescent on the lines of development of the typical ostiolate perithecium. Thus if the final stage in the development of the sterile sheath be omitted, namely the formation of the ostiole, the result is the imperforate perithecium from which a series of forms with degenerate hymenium may be derived as a consequence of the failure of the dehiscence mechanism. There are aparaphysate forms in which the paraphyses do not develop and forms with irregular hymenium, and if a regular mucilage cavity does not develop there results a cleistocarpic perithecium similar to the cleistocarpic apothecium. The development of the isolated perithecium is almost identical with that of the turbinulate apothecium and the process of juvenescence must in the long run produce similar forms in both Pyrenomycete and Discomycete series. It is a problem, indeed, how the true affinity of these derivative forms may be recognised. If the ascus is indehiscent it is impossible to distinguish an "operculate" cleistocarp from an "inoperculate" or one belonging to a Pyrenomycete, unless minor points of construction persist to indicate relationship. The characters of *Ncotiella Crozalsiana* are fortunately distinctive; it is in every respect other than the form of the apothecium a humariaceous Discomycete. But the characters of Inoperculeae are much less well defined and it is possible that some depauperate, xerophytic forms like *N. Crozalsiana* have been classed with Pyrenomycetes. The same proposition may arise in lichens, for the ascocarp of a degenerate

discolichen might similarly become perithecioid and be mistaken for that of a pyrenolichen. Church has extended his hypothesis to lichens (4), postulating the fruticose forms as *Cetraria* and *Usnea* as more primitive in respect of somatic organisation than the crustaceous and squamulose, and perhaps the simpler forms of thallus may also be derived by juvenescence from the more complex. In some instances, even, the two symbionts may have drifted apart and given birth to free-living "lichen-fungi" of both main groups of Ascomycete. *Karschia, Patinella, Calicium, Coniocybe* and other genera may represent such spurious Discomycetes and in the Mycosphaerellaceae may be found their Pyrenomycete anologues. The Patellariaceae, Stictidaceae and Protocaliciaceae may represent conglomerations of degenerate, disintegrated lichens and not relatives of such true Discomycetes as the Clavuleae, Ciboreae, etc. Lorrain Smith (13), however, maintains the upgrade standpoint of evolution and considers the Patellariaceae and Stictidaceae to be groups from which many series of lichens and Discomycetes have evolved. But there is no evidence yet that there has been an upgrade of this kind in Discomycetes, and these simply organised families are far more easily interpreted as products of degeneration. Watson (14) has also rejected Church's hypothesis in connection with lichens but he mentions a fact which falls in line with the hypothesis, namely, that the fruticose lichens generally have simple spores, whereas the squamulose and crustaceous forms chiefly have the septate, muriform and other derivative kinds. If the ascospore is the homologue of a zoid or a non-motile algal spore then the aseptate condition would be primitive and most likely to occur in lichens with the more primitive kinds of soma. It is much the same in Ascomycetes, notable exceptions being *Geoglossum* and other Clavuleae and *Cordyceps*. But, on the whole, elaboration of the ascospore goes with specialisation of the soma. The septate ascospore would appear to be an incipient germination in the confines of the ascus where nuclear division and the formation of cross-walls may occur, but not the extrusion of hyphae: the muriform ascospore then appears as a highly specialised condensed mycelium. On this interpretation also it is interesting to note that the ascus is one of the most conservative kinds of fungous sporangium, since it still develops virtually under water in the hymenial mucilage and still returns the plankton phase of asexual spore to the environment by hydrostatic discharge.

The similar development of the apothecium and the perithecium implies that the reduction series of Discomycetes, Pyrenomycetes and Lichen-fungi converge to the same limit in the cleistocarp, which must clearly find expression in the heterogeneous group of Plectascales. There is no kind of ascocarp in

this group which cannot be interpreted as a juvenile form of such origin. The figures *a–f* in Text-fig. 2 of the second paper of this series may be taken as diagrams of the naked ascus of *Endomyces*, the loose cleistocarp of *Gymnoascus*, the cleistocarp of *Aspergillus* with pseudoparenchymatous cortex but diffuse sporophytic system, and that of *Phyllactinia* with definite hymenium or some Pyrenomycete with imperforate perithecium. In the Erysiphaceae the best developed cleistocarps differ from the perithecium only in being imperforate and without a spacious mucilage cavity. The sterile sheath is formed round the sexual organs in the same way, but as it is reduced so it becomes more precise and specialised. In *Sphaerotheca Castagnei*, according to Hein (10), the sterile sheath is composed of a centripetal sympodium involving three sets of short hyphae, those of the final set being reduced to a single mucilage cell which Dangeard interprets as a paraphysis. *Sphaerotheca* is related to Pyrenomycetes very much as *Thelebolus* is to Discomycetes. There is one ascus in the cleistocarpic fructification in each, but in *Sphaerotheca* this ascus is evidently a penultimate cell of a short ascogenous hypha, whereas on analogy with the ascobolean archicarp it is the direct product of the ascogonium in *Thelebolus*. The mode of life of the Erysiphaceae so closely resembles that of *N. Crozalsiana* that clearly they must have evolved on the same lines and the erysiphaceous cleistocarp can be interpreted as a juvenile form of Pyrenomycete ascocarp. Even the appendages are explained more readily as juvenescent relics of the secondary mycelium than as its beginnings, which is the interpretation given by those who maintain the upgrade standpoint.

In the Gymnoascaceae the hyphae which invest the sexual organs do not combine to form a compact structure but the cleistocarp is loosely organised. The affinities of the group are obscure. The archicarps of *Amauroascus* and *Gymnoascus* resemble that of *Ascodesmis* and the coprophilous habit also recalls the Ascobolaceae. Boudier has placed *Aphanoascus* in the Pseudo-ascoboleae, though without stating definitely his reasons; the archicarp and the coprophilous habit suggest the Ascoboleae but the asci are indehiscent and scattered through the cleistocarp as in *Aspergillus*. At least the Gymnoascaceae are as readily interpreted as degenerate Pseudo-ascoboleae which have lost the power of constructing a complex tissue and thus their ascocarp does not develop beyond the equivalent of an early stage in the development of the ascobolean ascocarp; and *Aphanoascus* is perhaps a halfway house.

In the Endomycetaceae, Dipodascaceae, etc., both gametophytic and sporophytic systems of the ascocarp have dis-

appeared. There are no ascogenous hyphae and the sexual organs are not invested by a sterile sheath; the ascogonium becomes the ascus directly as in *Thelebolus*. Every factor in the construction of the ascocarp other than its merest beginning in the formation of the sexual organs has been lost and thus far reduction is complete. But the Saccharomycetaceae are still more degenerate. All factors of tissue formation have disappeared and the soma is virtually unicellular as an ascospore which continues to bud throughout its vegetative existence until it becomes itself both ascogonium and ascus, like the ascospores of *Exoascus* in artificial culture (11). The reversion of a race of organism once possessed of an elaborate equipment, involving a multaxial gametophyte with parasitic sporophyte, to the original plankton phase of unicellular existence, if true, is indeed a revelation of mycology, but, as Church points out, this transmutation is accompanied by one of equal magnitude in the environment. It is the morphological aspect of the passage of marine phytobenthos from autotrophic existence on a rocky shore to heterotrophy in the juices of land organisms.

As in Discomycetes biological evidence can be adduced in favour of the hypothesis of reduction. The fungi with isolated perithecia and cleistocarps, that is with minute fructifications, are characteristic of the specialised, the ephemeral and the depauperate habitats and they far outnumber in variety those with complex, massive fructifications. Church has already postulated in his view that Plectascales are fungi with degenerate ascocarps and the hypothesis of juvenescence shows how they may have arisen. In fact, given the development of the gametophytic system of the multaxial ascocarp and the special systems of the perithecium and apothecium, all other forms of ascocarp can apparently be deduced by the process of juvenescence. Nor does it matter in what order the juvenescence of the different parts is taken, for it seems also that all possible combinations have been fulfilled: speed and smallness, giving quick returns on little capital, are what matter, not appearances. There are monaxial stipitate apothecia with and without marginal growth and there are sessile apothecia with and without marginal growth: there are stromatic Pyrenomycetes with perforate and imperforate perithecia, with and without paraphyses, and there are isolated perithecia, paraphysate and aparaphysate: there are corticate cleistocarps with many asci and ones with a single ascus, while there are all manner of polyascial cleistocarps with various degenerate forms of sterile sheath, and finally those with a single ascus and no sheath. It is homoplasy on many different lines. Moreover, Church considers the Laboulbeniales juvenile expressions of Prefloridеae: that is, he considers them to have

degenerated before the transmigration and to have persisted in virtue of their rapid life-cycle as a most successful though most specialised phylum of Ascomycete. It is evident that in the phylogeny of Ascomycetes one has not a single kind of ancestor to consider but a whole phylum of seaweeds with its own multiplicity of degenerate and specialised forms. It is the essence of Church's hypothesis that it was an imperceptibly slow transmigration, or translation, of a marine vegetation *in situ* into subaerial environment, so that every kind of alga in that sea had the opportunity to establish itself on land. When subaerial existence inflicts heterotrophy, somatic deterioration and the loss of other characters of primary value in phyletic distinction, algae of diverse origin tend to the same end and one cannot hope to discover the affinity of any extant series by working backward from the present time. The broad outlines of the process can be indicated but each individual race had its own problems which were met in its own way. But for the fact that the different kinds of ascocarp of Pyrenomycetes, Discomycetes and Plectascales fit into the one scheme of degeneration every series of Ascomycete need not be derived from the same transmigrant form. By assuming, rather, an unbiassed outlook the meaning of Ascomycete is seen to acquire a new sense and is to be taken as the subaerial expression of a certain phylum of marine algae.

The present system of classifying genera and families of Pyrenomycetes and Plectascales is as artificial as that of Discomycetes being based largely on the form of the ascocarp and most of the classes include only fragments of the natural series. Several groups of Plectascales may belong to some major series of Ascomycetes covering all existing forms of ascocarp, but how such series can be recognised in Pyrenomycetes is far from clear. An obvious criterion like the paraphysial pigment in Operculeae is lacking though the investigation of the sexual organs and sporophytic system may disclose some fundamental property.

Discopodium.

A mycelium bearing one large ascocarp several centimetres high at least is assumed to be the primitive state of an Ascomycete, and a mycelium bearing many small ascocarps less than a millimetre high is assumed to be the derivative highly evolved state. Multiplication of the number of ascocarps per mycelium has accompanied degeneration of the ascocarp in accordance with the increased wastage factor in subaerial environment. The change has taken place in two main series, Discomycete and Pyrenomycete, which are distinguished by the form of the sporophytic fructification. The Discomycete has the massive

apothecium with broad open hymenium characteristically extended by marginal and intercalary growth. The origin of this property is unknown. It is well developed in those ascocarps which are here considered the more primitive, such as *Wynnea*, *Sarcoscypha* and *Sclerotinia*, and it is chiefly by deterioration of this property that the ascocarp has been reduced; it is lacking in immarginate and turbinulate apothecia which belong to highly specialised Discomycetes. So the property may be inherently primitive as a factor in the equipment of the "transmigrant Ascomycete" or an early response to the increased wastage encountered in the new environment.

The multaxial ascocarp of both series and the monaxial ascocarp of Pyrenomycetes produce many separate sporophytic fructifications. But the monaxial ascocarp of Discomycetes has only one such fructification which is terminal and gives in the first instance the stipitate apothecium. The monopoly of the axis by a terminal apothecium has evidently been decisive in the evolution of Discomycetes, whatever intermediates may have existed between multaxial and monaxial forms, and it has introduced its own peculiar series of reduction forms. A special term for this form of ascocarp would be convenient and "discopodium" suggests itself as appropriate and self-explanatory. It is suitable because it does not distinguish between stipitate and sessile apothecia, both of which are possessed of an axis or primary shaft of hyphae. It covers also the case of *Helvella* or *Rhyparobius* as well as of *Geoglossum* or *Pyronema*, in which the ascocarp corresponds to the axile portion only, and it emphasises the essential continuity of the hyphal systems of the ascocarp. No break occurs between the formation of the sterile axis and the development of the sporophyte such as there is in the Florideae, where the soma has a preliminary vegetative phase before it breaks out into cystocarps. The soma of the Ascomycete is merely a fructification or a hyphal system destined to reproduce the race, and only with a complete knowledge of the development of this system can one discover the interrelations of the different forms of ascocarp. In Discomycetes this system has become a mechanism for the expulsion of ascospores from the whole of a discoidal surface, and the form of the mechanism is determined by an initial period of upgrowth of a shaft of hyphae and a subsequent period of expansion of the apex by marginal and intercalary growth, during which period the system of the sporophyte develops: and this it is proposed to call the discopodium. Several terms are used in systematic works to describe the Discomycete ascocarp, but they scarcely meet the case. Ascocarp, ascoma, receptacle, fruit body are used generally for the whole structure, stroma for the sterile part and apothecium

for the fertile part, or simply the expressions sessile and stipitate apothecium may be used. They do not imply the essential feature of this ascocarp, namely that it is monaxial and typically symmetrical about the one axis.

Over 99 per cent. of the ascocarps of living Discomycetes are variants of the discopodium, which is remarkable because the hypothesis of reduction requires that the final state of all Ascomycetes should be that attained by the Endomycetaceae or Saccharomycetaceae or at least the Plectascales, namely extreme simplification by elimination of superfluous sterile tissue and thus with a minimum of environmental restriction. The number of Ascomycetes with such simple ascocarps is relatively small and perhaps sufficient time has not elapsed for the full evolution of the group, though it is more likely that the various forms of ascocarp have each their biological value and that the discopodium is therefore a more or less permanent phase of the Discomycete ascocarp. For instance, a lenticular apothecium may have reverted to a sessile cupular or stipitate form and survived if reproductive advantages accrued therefrom, and the possibility shows how endless complications may be imposed upon the simple scheme and that each individual case must be judged on its own merits.

Certain forms of discopodium have been described already on the basis of the gametophytic system, but they are provisional and not exact. A comprehensive classification must include the sporophytic system and a few points may be considered in this respect. The sporophytic system is the set of ascogenous hyphae in an apothecium. It develops typically from one or more distinct cells which are the ascogonia and are considered homologous, or at any rate comparable, with the carpogonia of Florideae, inasmuch as they are the mother cells of the diploid sporophyte. The state of the system is varied. It may be simple or compound according as it arises from one or more ascogonia, and may be exogenous or endogenous according to the time of formation of the ascogonia. It may be called exogenous if the ascogonia develop before the gametophytic system and are borne on the mycelium, and endogenous if the ascogonia develop later inside the gametophytic system. In large cupular apothecia the sporophytic system forms a network several square centimetres in extent, but in the smallest apothecia it may be limited to a few cells. Claussen found that in *Ascodesmis nigricans* three ascogenous hyphae of very few cells arose from the ascogonium and each produced a single ascus, while in a species of *Rhyparobius*, according to de Bary (7), Borzi found that each shoot from the ascogonium became an ascus directly; and then there is *Thelebolus*. Moreover, there is variety in the branching of the

ascogenous hyphae and in the production of asci, and a sporophytic system may develop through more than one phase, *e.g. Pyronema*. Perhaps the differences are also an outcome of juvenescence, for reduction in length of the ascogenous hyphae expresses early cessation of growth, cf. *N. Crozalsiana*, and if early enough the asci of a complex system may be borne in a premature phase.

The sporophytic system is endogenous and compound in all stipitate apothecia which have been examined, namely *Cudonia lutea*, *Spathularia velutipes*, *Trichoglossum hirsutum*, *Rhizina inflata*, *Helvella crispa*, *H. elastica*, and probably *Leotia lubrica*, *L. atrovirens*, *Mitrula phalloides* and *M. pusilla*. On the homology with the cystocarp each apothecium represents originally the product of one fertilisation, so that the simple sporophytic system should be primitive. That this is not so in existing forms of ascocarp which are considered the more primitive can be explained by assuming that the gametophytic system has degenerated more rapidly than the sporophytic system. The sporophytic system is compound with respect to the soma of the multaxial ascocarp, and it would not unnaturally persist as compound on reduction of the soma to a single axis and terminal disc. Yet the apothecium may have been originally compound, cf. Corallinaceae, and it is with all the more interest therefore that one waits the investigation of *Wynnea*.

In all sessile apothecia which have been examined the sporophytic system is exogenous and either compound as in *Pyronema* or simple as in *Ascobolus*. The system thus becomes a unit derived from an initial hypha called the archicarp on account of its conspicuous nature. The gametophytic system here is post-sexual and proceeds directly to the formation of the apothecium. Unfortunately an intermediate state with the merest relic of a pre-sexual soma has not been discovered; *Acetabula*, *Disciotis* or *Sarcoscypha* might afford examples. In the smallest forms of sessile apothecium, namely the cleistocarpic and perithecioid, the characteristics of the discopodium are lost, and such forms become convergent with reduction forms of Pyrenomycetes in which the gametophytic system is similarly restricted in the long run to a post-sexual phase and an archicarp commences the fructification. Now this cleistocarpic structure has been homologised with the cystocarp, and as in each the fructification represents a parasitic diploid sporophyte composed of filaments bearing sporangia and enveloped by a post-sexual sterile sheath of haploid gametophytic filaments, the homology may stand. But it must be remembered that at least in Discomycetes these simple ascocarps can be interpreted as juvenile expressions of a multaxial form, which is comparable not with the cystocarp but

with the whole plant, vegetative soma and cystocarps, of a red alga.

A reservation must likewise be introduced in the homology between the ascogonial hypha or archicarp and the procarp. In cleistocarps, sessile apothecia and isolated perithecia the sporophytic system is derived from a hypha of the first order, yet on the interpretation here given the system must have been borne originally on an axis of high order, and in these juvenile forms it need not necessarily repeat in any high degree the ancestral construction. One must postulate a system of generative hyphae in ascocarps with an endogenous sporophytic system, even if it cannot always be made visible, cf. Leotiaceae, because not every hypha bears an ascogonium. Originally the ascogonium was borne on hyphae of a high order in the multaxial ascocarp, but this order is reduced by precocious maturing of the ascocarp and, whatever the primitive position of the ascogonium, terminal or intercalary, clearly it may happen that the parent cell of the ascogonial hypha becomes itself the ascogonium, which is then intercalary on the generative hypha with a distal sterile portion. The process may be repeated till the ascogonium is borne on a hypha of the first order, and the "septate trichogyne" and the archicarp can then be explained as products of the juvenescence of the sporophytic system without recourse to doubtful homology with the floridean procarp. None of these Discomycetes in which the sexual organs have been examined can be regarded as primitive, and even though the "septate trichogyne" appears in a stipitate apothecium, *e.g. Cudonia*, that does not mean that it is a primitive structure; the soma is already heterotrophic and much reduced and must therefore be discussed in terms of hyphae. Evidence is yet lacking of the primitive state of the ascogonium or oogonial ramulus in Discomycetes. One may argue perhaps from Laboulbeniaceae and those lichens which possess a functional "trichogyne," but nevertheless the construction of the archicarp in reduced and specialised Discomycetes such as Pyrenomaceae, Ascobolaceae, Humariaceae, Pezizaceae, etc., like the construction of the soma, cannot be properly understood until the respective hyphal systems are known in the larger and less reduced forms.

These studies in Discomycetes have arisen from an investigation of the bryicolous parasite *Neotiella Crozalsiana*. It was found that the perithecioid fruit body of this aberrant fungus was but a persistently juvenile form of angiocarpic lenticular apothecium and that it was merely a specialised member of the Humariaceae. But in this case of arrested development was

perceived a process which would account naturally for the evolution of the known forms of Discomycete ascocarp. The hypothesis which has been developed leads to conclusions about the origin of Ascomycetes much at variance with the opinions of mycologists in general, but at least a consistent and comprehensive story has resulted. It is surprising how little is known of these fungi. They are still chiefly the objects of specification and recollection and they are better known in cytological than biological aspect, and less than 1 per cent. have been examined cytologically. Still some are among the commonest fungi and the Operculeae have much to recommend their study. The large size of the tissue elements and reproductive organs and the crisp turgid consistency facilitate microscopic examination to such an extent that freehand sections and a few taps on the coverslip will disclose more detail of the hyphal systems than a series of microtome sections. It seems that in the Operculeae one may discover natural series and thus may gain an idea of phyletic progression in Ascomycetes.

Summary.

Current views on the evolution of Ascomycetes are considered. Church's hypothesis of evolution from complex marine phytobenthos is upheld because it explains the origin of the multaxial ascocarp which the hypothesis of juvenescence postulates as the primitive form of ascocarp in Discomycetes. Conclusions drawn from phycology and mycology are in agreement and the multaxial ascocarp is homologised with a multaxial cable type of algal soma bearing numerous parasitic filamentous sporophytes. The postulate presupposes a massive autotrophic vegetation and the hypothesis of juvenescence supports Church's hypothesis of subaerial transmigration of marine phytobenthos.

It is shown that in Pyrenomycetes the simple forms of ascocarp can also be interpreted as juvenile expressions of a multaxial form. It is considered that Pyrenomycete and Discomycete series converge to the limit of the cleistocarp and that the Plectascales are degenerate members of both series. A juvenescent series can be traced from the multaxial ascocarp to the condition of the yeast plant which never becomes a multicellular organism. The difficulty in recognising degenerate cleistocarpic forms of operculate and inoperculate Discomycetes, Pyrenomycetes and possibly Lichen fungi is indicated.

The upgrade theory of the evolution of Discomycetes from Plectascales is considered untenable because evidence is lacking that any simple form of ascocarp belongs to a primitive Discomycete: it ignores the similarity in the factors of equipment of Discomycetes and marine phytobenthos and it lacks biological

support. Likewise the exponents of the origin of Ascomycetes from Florideae fail to recognise the importance of somatic organisation and deal only with forms of ascocarp which are considered reduced and juvenile. While Ascomycetes cannot be referred to any algal series they embody to some extent the equipment of Prefloridèae.

The term "discopodium" is suggested for the monaxial ascocarp of Discomycetes.

The state of the sporophytic system of the discopodium is briefly considered.

In conclusion the writer must express his deep obligation to Mr J. Ramsbottom, of the British Museum, who kindly undertook the supervision and publication of these papers, and to Dr A. H. Church, of Oxford University, for the occasions on which he has discussed the problems of fungi and the origin of the land flora.

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PROCEEDINGS, 1929–30

MEETING. UNIVERSITY COLLEGE, LONDON. *23rd November*, 1929.

R. R. Gates and D. V. Daran. Zygospore formation in Mucors.

J. Grove. Growth reactions of *Helotium scutula* Karst.

R. G. Tomkins. The relation of mould growth to humidity.

H. Wormwald. Some recent observations on brown-rot diseases of fruit.

E. C. Barton-Wright. Sexual reproduction in *Penicillium*.

MEETING. UNIVERSITY COLLEGE, LONDON. *1st February*, 1930.

B. Barnes. Induced variations in *Thamnidium elegans*.

G. Samuel. The generic names *Alternaria* and *Macrosporium*.

H. S. Vasudeva. The effect of one organism in reducing the virulence of another.

W. Brown. Investigations on the physico-chemical basis of disease resistance.

I. Reichert. Infection of *Aegilops* with *Tilletia*.

MEETING. UNIVERSITY COLLEGE, LONDON. *29th March*, 1930.

E. M. Blackwell and G. M. Waterhouse. Spores and spore germination in the genus *Phytophthora*.

M. Brett. *Stemphylium-Alternaria*.

K. St G. Cartwright. The study of Basidiomycetes in culture.

S. Dickinson. The genetics of the Smut Fungi.

S. P. Wiltshire. The preservation of Petri dish cultures of Fungi (Exhibit).

MEETING. UNIVERSITY COLLEGE, LONDON. *15th November*, 1930.

A. H. R. Buller and H. J. Brodie. The development and function of the oidia of the Hymenomycetes.

A. H. R. Buller and S. E. Downing. The dwarf spores of *Pleurage anserina*.

D. V. Daran. Studies in the life history of *Dicranophora*.

D. V. Daran. Reproductive processes in the Mucorineae.

E. Green. The germination of spores of Ascobolaceae.

P. H. Harrison. Some notes on an interesting Discomycete, *Sclerotinia aestivale* Pollock.

SPRING FORAY FOR STUDENTS, BYFLEET. *10th May*.

SPRING FORAY, KING'S LYNN. *6th–10th June*.

AUTUMN FORAY, WHITBY. *15th–20th September*.

AUTUMN FORAY FOR STUDENTS, OXSHOTT. *4th October*.

FORAY WITH ESSEN FIELD CLUB, EPPING FOREST. *11th October*.

FORAY WITH BRITISH ECOLOGICAL SOCIETY, TRING. *18th October*.

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3. Adcock, Mr Archie, Upton Road, Norwich. (1921.)
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5. Ali, Mr M. N., Forestry Department, H.E.H. The Nizam's Dominions, Hyderabad, India. (1926.)
6. Allen, Miss I. M., 4, Cunningham Avenue, St Albans, Herts. (1922.)
7. Ashby, Mr S. F., B.Sc., Imperial Bureau of Mycology, 17, Kew Green, Kew, Surrey. (1926.)
8. Ashford, Dr Bailey K., Professor of Tropical Medicine and Mycology, University of Porto Rico, Box 887, San Juan, Porto Rico, W.I. (1929.)
9. Baker, Mr Thomas, 191, Lees Road, Oldham. (1923.)
10. Barnes, Mr B., Ph.D., Birkbeck College, Bream's Buildings, Chancery Lane, London, E.C. 4. (1922.)
11. Barnett, Miss E. C., B.Sc., West of Scotland Agricultural College, 6, Blythswood Square, Glasgow. (1921.)
12. Barr, Rev. Robert, T.D., M.A., The Manse, Neilston, Renfrewshire. (1918.)
13. Barrington, Dr F. J. F., University College Hospital, Medical School, University Street, London, W.C. 1. (1901.)
14. Bartlett, Mr A. W., M.A., B.Sc., Department of Botany, Armstrong College, Newcastle-on-Tyne. (1920.)
15. Bates, Mr G. R., c/o British South Africa Company, Mazoe Citrus Estate, Mazoe, S. Rhodesia. (1930.)
16. Bates, Mrs L. F., B.Sc., 36, Gainsborough Gardens, Golders Green, London, N.W. 11. (1921.)
17. Beaumont, Mr Albert, M.A., Seale-Hayne Agricultural College, Newton Abbot, Devon. (1924.)

18. Bewley, Mr W. F., D.Sc., Experimental and Research Station, Cheshunt, Herts. (1922.)
19. Biffen, Professor Sir Rowland H., M.A., F.R.S., 136, Huntingdon Road, Cambridge. (1899.)
20. Biologist, Plant Research Laboratory, Horticultural Gardens, Burnley, Victoria, Australia. (1921.)
21. Birmingham Natural History and Philosophical Society, c/o G. T. Calvert, Esq., Hon. Librarian, Avebury House, 55, Newhall Street, Birmingham. (1920.)
22. Bisby, Mr Guy R., Ph.D., Manitoba Agricultural College, Winnipeg, Canada. (1921.)
23. Blackman, Professor V. H., M.A., F.R.S., Imperial College of Science, South Kensington, London, S.W. 7. (1900.)
24. Blackwell, Miss Elsie M., M.Sc., Botanical Department, Royal Holloway College, Englefield Green, Surrey. (1917.)
25. Blagden, Mr C. O., School of Oriental Studies, Finsbury Circus, London, E.C. 2. (1910.)
26. Bloom, Mr James Harvey, M.A., 36, Ryde Vale Road, Balham, London, S.W. 12. (1915.)
27. Bolas, Mr B. D., 20, Cambridge Gardens, Winchmore Hill, London, N. 21. (1924.)
28. Borthwick, Professor A. W., O.B.E., D.Sc., Forestry Department, The University, Aberdeen. (1911.)
29. Boston, The Mycological Club, c/o Miss Jennie F. Conant, 26, Prospect Street, Melrose, Mass., U.S.A. (1906.)
30. Bradshaw, Mr F., M.A., D.Sc., Armstrong College, Newcastle-on-Tyne. (1928.)
31. Braid, Professor K. W., B.A., B.Sc., West of Scotland Agricultural College, 6, Blythswood Square, Glasgow. (1922.)
32. Brazier, Mr E., Ty'n-y-gongl, Love Lane, Stourbridge. (1921.)
33. Brenchley, Mr G. H., B.A., Clare College, Cambridge. (1925.)
34. Brett, Miss M., M.Sc., Northern Polytechnic, Holloway Road, London, N. 7. (1921.)
35. Briant, Mr A. K., B.A., Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I. (1927.)
36. Brierley, Mr W. B., D.Sc., F.R.A.I., F.L.S., Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts. (1919.)
37. Bright, Mr T. B., B.A., Chucks Cottage, Walton-on-the-Hill, Surrey. (1927.)
38. Brisbane, The Director, Bureau of Sugar Experiment Stations, Department of Agriculture and Stock, Queensland, Australia. (1930.)
39. British Museum, The Trustees of, Cromwell Road, South Kensington, London, S.W. 7. (1914.)

40. Briton-Jones, Professor H. R., D.Sc., Ph.D., D.I.C., A.R.C.S., Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I. (1923.)
41. Brooks, Mr F. T., M.A., The Botany School, Cambridge. (1907.)
42. Brown University, Library, East Side Station, Providence, R.I., U.S.A. (1920.)
43. Brown, Professor W., M.A., D.Sc., Imperial College of Science, South Kensington, London, S.W. 7. (1922.)
44. Bruxelles, Jardin Botanique de l'État, c/o M. P. van Aerdschot. (1911.)
45. Bryce, Mr G., D.Sc., Department of Agriculture, Ibadan, Nigeria, W. Africa. (1915.)
46. Buckley, Mr W. D., "Lynmouth," 2, Curzon Street, Slough. (1916.)
47. Buddin, Mr Walter, M.A., Laboratory of Plant Pathology, University of Reading, 7, Redlands Road, Reading. (1921.)
48. Buller, Professor A. H. R., D.Sc., Ph.D., F.R.S., University of Manitoba, Winnipeg, Canada. (1911.)
49. Bunker, Mr H. J., B.A., "Lindau," Hatherden Avenue, Danecourt Road, Parkstone, Dorset. (1925.)
50. Bunting, Mr R. H., F.L.S., Imperial College of Science, Biological Field Station, "Hurworth," London Road, Slough. (1921.)
51. Bunyard, Mr G. N., F.L.S., 25, Bower Mount Road, Maidstone, Kent. (1920.)
52. Burgess, Mr R., M.Sc., British Research Association for the Woollen and Worsted Industries, Torridon, Headingley, Leeds. (1928.)
53. Burr, Mr S., The Agricultural Department, The University, Leeds. (1924.)
54. Butcher, Mr R. W., B.Sc., Fisheries Research Station, Alresford, Hants. (1922.)
55. Butler, Mr E. J., C.I.E., D.Sc., F.R.S., M.B., F.L.S., Imperial Bureau of Mycology, 17, Kew Green, Kew, Surrey. (1920.)
56. Butler, Mr R. R., M.Sc., A.I.C., Chemical Department, Municipal Technical School, Plymouth, Devon. (1924.)
57. Cadman, Miss E. J., c/o Mackay, 111, Dudley Avenue, Leith, near Edinburgh. (1921.)
58. Cambridge, The Botany School. (1920.)
59. Carne, Mr W. M., F.L.S., Department of Agriculture, Perth, Western Australia. (1928.)
60. Carr, Professor J. W., M.A., Public Natural History Museum, Wollaton Hall, Nottingham. (1896.)
61. Carrothers, Mr E. N., 145, Stranmillis Road, Belfast, N. Ireland. (1925.)
62. Carter, Miss Nellie, D.Sc., Botanical Department, East London College, Mile End Road, London, E. (1929.)

63. Cartwright, Mr K. St G., B.A., The Red House, Kingston Blount, Oxford. (1913.)
64. Castellani, Sir Aldo, M.D., 33, Harley Street, London, W. 1. (1922.)
65. Cayley, Miss Dorothy M., John Innes Horticultural Institute, Mostyn Road, Merton, Surrey. (1913.)
66. Cejp, Dr Karel, Na Slupi 433, Praha (Prague) II, Czechoslovakia. (1930.)
67. Chapman, Mr A. Chaston, F.R.S., F.I.C., Chemical Laboratories, 8, Duke Street, London, E.C. 3. (1926.)
68. Charles, Mr J. H. V., Biochemical Laboratory, Ardeer Factory, Nobel's Explosives Co., Ltd., Stevenston, Ayrshire. (1922.)
69. Chaudhuri, Mr H., M.Sc., Ph.D., University of the Punjab, Lahore, India. (1920.)
70. Cheal, Mr W. F., Kirton Agricultural Institute, Kirton, Nr Boston, Lincs. (1927.)
71. Cheel, Mr Edwin, Botanic Gardens, Sydney, New South Wales, Australia. (1919.)
72. Chona, Mr B. L., Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1929.)
73. Ciferri, Dr R., P.O. Box 113, Santiago, Dominican Republic, W.I. (1926.)
74. Cleland, Mr J. Burton, M.D., Professor of Pathology, University of Adelaide, South Australia. (1918.)
75. Clement, Mr E., The Cottage, Yew Tree Road, Southborough, Kent. (1927.)
76. Connecticut Agricultural Experiment Station, New Haven, Connecticut, U.S.A. (1929.)
77. Cook, Mr W. R. I., Ph.D., Department of Botany, The University, Bristol. (1924.)
78. Cooper, Miss Charlotte A., California Lane, Bushey Heath, Herts. (1911.)
79. Cooper, Mrs V. Astley, Clerdoun, Epsom Road, Ewell, Surrey. (1921.)
80. Copenhagen, Universitets-Bibliothek, c/o P. Haase & Son, Løvstraede 8, København K., Denmark. (1923.)
81. Cornell University, The Library, New York State College of Agriculture, Ithaca, N.Y., U.S.A. (1920.)
82. Corner, Mr E. J. H., B.A., Assistant Director, Botanic Garden, Singapore, Straits Settlements. (1924.)
83. Cotton, Mr Arthur D., F.L.S., Keeper, Herbarium, Royal Botanic Gardens, Kew, Surrey. (1902.)
84. Crawford, Miss J. M., The Vicarage, Lyford Road, Wandsworth Common, London, S.W. 18. (1926.)
85. Crow, Mr W. B., M.Sc., Ph.D., F.L.S., Department of Biology, Technical College, Huddersfield. (1921.)

86. Cunningham, Mr G. H., Ph.D., Plant Research Station, Box 240, Palmerston North, New Zealand. (1922.)
87. Curtis, Miss Kathleen M., M.A., D.Sc., D.I.C., F.L.S., Mycologist, Biological Department, Cawthron Institute of Scientific Research, Nelson, New Zealand. (1917.)
88. Cutting, Mr E. M., M.A., F.L.S., Botanical Department, University College, Gower Street, London, W.C. 1. (1920.)
89. Dade, Mr H. A., A.R.C.S., Department of Agriculture, Aburi, Gold Coast, West Africa. (1927.)
90. Darbishire, Professor O. V., B.A., Ph.D., F.L.S., The University, Bristol. (1913.)
91. Das, Mr Kedarnath, C.I.E., M.D., Principal, Carmichael Medical College, 1, Belgachia Road, Calcutta, India. (1922.)
92. Davies, Mr D. W., B.Sc., Adviser in Mycology, Agricultural Buildings, University College of Wales, Aberystwyth. (1923.)
93. Davies, Miss E. M., B.Sc., Woodford School, East Croydon, Surrey. (1928.)
94. Davis, Mr J. Jefferson, B.S., M.D., University of Wisconsin, Madison, Wis., U.S.A. (1921.)
95. Day, Mr E. Metcalfe, Rowan Cottage, Minchinhampton, Glos. (1921.)
96. Day, Mr W. R., B.A., B.Sc., Imperial Forestry Institute, Oxford. (1928.)
97. Dehra Dun, The Forest Botanist, Forest Research Institute and College, U.P., India. (1929.)
98. Deighton, Mr F. C., M.A., Mycologist, Department of Lands and Forests, Freetown, Sierra Leone, West Africa. (1925.)
99. Dickinson, Mr S., Botanical Department, University College, Cardiff, S. Wales. (1921.)
100. Dickson, Mr B. T., B.A., Ph.D., Senior Mycologist, Council for Scientific and Industrial Research, 314, Albert Street, East Melbourne, Australia. (1923.)
101. Dodge, Dr Carroll W., Farlow Herbarium, 20, Divinity Avenue, Cambridge 38, Mass., U.S.A. (1926.)
102. Dowson, Mr W. J., M.A., D.Sc., Department of Agriculture, Launceston, Tasmania. (1920.)
103. Duncan, Mr J. T., London School of Hygiene and Tropical Medicine, Keppel Street, London, W.C. 1. (1930.)
104. East African Agricultural Research Station, Amani, *via* Tanga, Tanganyika Territory, East Africa. (1929.)
105. Edwards, Mr W. H., Belle Vue, Barline, Beer, Devon. (1896.)
106. Elliot, Rev. E. A., Great Longstone, Derbyshire. (1923.)
107. Elliott, Mr W. T., D.D.S., L.D.S., F.L.S., F.Z.S., Arden Grange, Tanworth-in-Arden, Warwickshire. (1913.)
108. Elliott, Mrs J. S. Bayliss, D.Sc. (B'ham), B.Sc. (Lond.), Arden Grange, Tanworth-in-Arden, Warwickshire. (1911.)

109. Ellis, Mr E. H., Department of Botany, British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7. (1924.)
110. Ellis, Miss E. M., St Hugh's College, Oxford. (1930.)
111. Ellis, Mr Holmes, F.R.M.S., 23, Townley Street, Colne, Lancs. (1927.)
112. Emoto, Dr Y., Tokugawa Biological Institute, Ebara-Gun, Tokyo-Fu, Japan. (1929.)
113. Engledow, Professor F. L., M.A., School of Agriculture, Cambridge. (1922.)
114. Essex Field Club, c/o Mr Percy Thompson, F.L.S., Essex Museum of Natural History, Romford Road, Stratford, London, E. 15. (1919.)
115. Exeter, Librarian, University College of the South-West of England. (1926.)
116. Eyre, Miss J. C., Maitlands Cottage, Ipplepen, Newton Abbot, Devon. (1915.)
117. Faulkner, Mr F., c/o Gillanders, Arbuthnot & Co., Bombay, India. (1930.)
118. Fenton, Mr E. W., M.A., B.Sc., F.L.S., Biology Department, Edinburgh and East of Scotland College of Agriculture, Edinburgh. (1920.)
119. Fikry, Mr Amin, Plant Protection Section, Cotton Research Board, Giza, Egypt. (1927.)
120. Findlay, Mr W. P., B.Sc., A.R.C.S., Courte Falaise, Sevenoaks, Kent. (1928.)
121. Finlayson, Mr Raymond A., F.L.S., Official Seed Testing Station, Huntingdon Road, Cambridge. (1910.)
122. Forwood, Mr R., Wynfield, Parkgate, Cheshire. (1930.)
123. Fry, Miss E. J., "Hazlehurst," Pear Tree Avenue, Bitterne, Southampton. (1923.)
124. Gadd, Mr C. H., D.Sc., Tea Research Institute, Nuwara Eliya, Ceylon. (1921.)
125. Galloway, Mr L. D., 2, Milton Crescent, Cheadle, Cheshire. (1928.)
126. Gardner, Capt. Frederic, c/o Barclays Bank, Jersey, C.I. (1898.)
127. Garside, Mr S., M.Sc., F.L.S., Botanical Department, Bedford College, Regent's Park, London, N.W. 1. (1922.)
128. Gates, Professor R. R., B.Sc., Ph.D., F.L.S., King's College, Strand, London, W.C. 2. (1921.)
129. Gäumann, Dr E. A., Prof. f. spezielle Botanik, Universitätsstrasse 2, Zürich 6, Switzerland. (1928.)
130. Gilbert, Dr E. M., Botanical Department, University of Wisconsin, Madison, Wis., U.S.A. (1922.)
131. Gilbert, M. E., Docteur en Pharmacie, 6, Rue de Laos, Paris (15e), France. (1924.)
132. Glasstone, Mrs V. F. C., B.A. (Oxon.), 15, Northumberland Road, Sheffield. (1930.)

133. Gorman, Mr M. J., A.R.C.Sc.I., Albert Agricultural College, Glasnevin, Dublin. (1925.)
134. Gough, Mr G. C., B.Sc., A.R.C.S., Ministry of Agriculture, Cornwall Buildings, 45, Newhall Street, Birmingham. (1923.)
135. Gould, Mr F. G., Woodrising, Trapps Hill, Loughton, Essex. (1918.)
136. Green, Col. C. Theodore, A.M.S., M.R.C.S., L.R.C.P., F.L.S., 31, Shrewsbury Road, Birkenhead. (1901.)
137. Green, Miss E., 15, Gower Street, London, W.C. 1. (1925.)
138. Gregor, Mrs J. F., Royal Botanic Garden, Edinburgh. (1927.)
139. Gregory, Dr P. H., 16, York Avenue, Hove, Sussex. (1930.)
140. Grinling, Mr C. H., B.A., 71, Rectory Place, Woolwich, London, S.E. 18. (1913.)
141. Grove, Miss Jessica H., 14, The Tything, Worcester. (1927.)
142. Gwynne-Vaughan, Professor Dame Helen, D.Sc., LL.D., F.L.S., 93, Bedford Court Mansions, London, W.C. 1. (1906.)
143. Hall, Miss M. P., Plant Pathology Department, Imperial College of Science, South Kensington, London, S.W. 7. (1930.)
144. Hanna, Mr W. F., M.Sc., Dominion Rust Research Laboratory, Agricultural College, Winnipeg, Canada. (1925.)
145. Hansford, Mr C. G., M.A., Mycologist, Department of Agriculture, Kampala, Uganda. (1921.)
146. Harris, Mr R. V., B.Sc., Horticultural Research Station, East Malling, Kent. (1924.)
147. Harvard University, The Library, Cambridge, Mass., U.S.A. (1923.)
148. Hastings, Mr Somerville, M.S., F.R.C.S., 43, Devonshire Street, Portland Place, London, W. 1. (1913.)
149. Heim, M. Roger, Assistant au Muséum d'Histoire Naturelle, 63, Rue de Buffon, Paris (V^{e}), France. (1930.)
150. Hemmi, Dr Takewo, Phytopathological Institute, Department of Agriculture, Kyoto Imperial University, Kyoto, Japan. (1923.)
151. Hildyard, Mr F. W., 14, Lambridge, Bath. (1913.)
152. Hoggan, Miss I. A., Department of Plant Pathology, University of Wisconsin, Madison, Wis., U.S.A. (1923.)
153. Holden, Professor H. S., F.L.S., Botanical Department, University College, Nottingham. (1923.)
154. Honolulu, Association of Hawaiian Pineapple Canners, P.O. Box 3166, Hawaii. (1929.)
155. Honolulu, The Library, Experiment Station, S.P.A., Box 411, Hawaii. (1920.)
156. Hopkins, Mr J. C. F., Agricultural Department, Salisbury, S. Rhodesia. (1930.)

157. Horne, Mr A. S., D.Sc., F.L.S., F.G.S., Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1921.)
158. Howard, Mr H. J., F.R.M.S., "Lingfield," 6, College Road, Norwich. (1918.)
159. Howarth, Mr W. O., M.Sc., Botanical Department, The University, Manchester. (1927.)
160. Hughes, Mr G. C., Chesterton, Bicester, Oxon. (1898.)
161. Hughes, Mr J. S., University Observatory, Oxford. (1927.)
162. Hull, The Librarian, Botanical Department, University College. (1929.)
163. Humphrey, Mr C. J., Mycologist and Plant Pathologist, Bureau of Science, Manila, Philippine Islands. (1921.)
164. Hunter, Mrs R., Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I. (1925.)
165. Hurrell, Mr H. E., 25, Regent Street, Great Yarmouth. (1921.)
166. Hurst, Mr C. P., Bedwyn, Wilts. (1928.)
167. Imperial College of Tropical Agriculture, Trinidad, B.W.I. (1921.)
168. Iowa, The Library, State University of Iowa, Iowa City, U.S.A. (1923.)
169. Iowa State College, Library, Ames, Iowa, U.S.A. (1927.)
170. Issatchenko, Professor B. L., Directeur du Jardin Botanique, Leningrad, Russia. (1923.)
171. Jaczewski, Professor Arthur de, Director, Institute of Mycology and Phytopathology, Perspective Anglaise 29, Leningrad, Russia. (1922.)
172. John Crerar Library, 86, East Randolph Street, Chicago, Illinois, U.S.A. (1929.)
173. John Innes Horticultural Institute, Mostyn Road, Merton, Surrey. (1924.)
174. Johnson, Mr J. W. Haigh, M.Sc., F.I.C., F.L.S., Walton, Nr Wakefield. (1919.)
175. Johnstone, Miss K. H., B.A., All Saints' Vicarage, Cheltenham, Glos. (1927.)
176. Johnstone, Mr R. B., 3, Oswald Gardens, Scotstounhill, Glasgow. (1908.)
177. Jones, Mr G. H., M.A., Plant Protection Section, Ministry of Agriculture, Cairo, Egypt. (1922.)
178. Jones, Mr Robert Fowler, Trinity House, Denton Road, Ilkley, Yorks. (1918.)
179. Jørstad, Mr Ivar, Statsmykolog, Botanisk Museum, Oslo, Norway. (1923.)
180. Kavina, Professor Dr Karel, Professor of Botany, Havlickovy-sady 58, Praha-Kral. Vinohrady (Prague), Czechoslovakia. (1926.)

181. Keilin, Dr D., Molteno Institute of Parasitology, Cambridge. (1922.)
182. Keissler, Dr Karl, Direktor d. Botanischen Abteilung, Naturhistorisches Museum, Burgring 7, Wien 1/1, Austria. (1924.)
183. Kelly, Dr Howard A., 1418, Eutaw Place, Baltimore, Md., U.S.A. (1921.)
184. Kidd, Mrs Franklin, B.A., The Botany School, Cambridge. (1919.)
185. Klika, Mr Bohumil, Hálkova 37, Prague, Vrsovice 553, Czechoslovakia. (1926.)
186. Kniep, Professor Dr H., Botanisches Laboratorium, Freiburg, Germany. (1930.)
187. Knight, Mr H. H., M.A., The Lodge, All Saints' Villas, Cheltenham. (1914.)
188. Knowles, Miss M. C., M.R.I.A., Natural History Museum, Dublin. (1925.)
189. Krieger, Mr L. C. C., 2114, N. Calvert Street, Baltimore, Md., U.S.A. (1921.)
190. Kuala Lumpur, F.M.S., The Director of Agriculture, Straits Settlements, and Federated Malay States. (1930.)
191. Lampitt, Mr L. H., D.Sc., F.I.C., Thornlea, Mount Park, Harrow, Middlesex. (1925.)
192. Leach, Mr R., B.A., Agricultural Department, Zomba, Nyasaland. (1929.)
193. Lee, Miss E. M., 55, Logan Road, Bishopston, Bristol. (1929.)
194. Leicester, The Museum, City of Leicester. (1923.)
195. Lewis, Professor F. J., D.Sc., University of Alberta, Edmonton, Alberta, Canada. (1924.)
196. Line, Mr James, M.A., School of Agriculture, Cambridge. (1921.)
197. Linnean Society, The, Burlington House, Piccadilly, London, W. 1. (1919.)
198. Lloyd Library, The, Cincinnati, Ohio, U.S.A. (1907.)
199. Loader, Miss F. M., Botanical Department, University College, Southampton. (1927.)
200. Lowndes, Mr A. G., M.A., Marlborough College, Marlborough, Wilts. (1922.)
201. Macdonald, Mr J., 25, Drumsheugh Gardens, Edinburgh. (1929.)
202. Mackenzie, Miss A. D., Research Station, East Malling, Kent. (1921.)
203. Madras University Library, Senate House, Triplicane, Madras, South India. (1925.)
204. Maire, M. René, D.Sc., Professeur à la Faculté des Sciences de l'Université, Algiers, Algeria, N. Africa. (1907.)
205. Maltby, Mr G. C., 14, Northwick Road, Evesham. (1923.)
206. Mandalay, Burma, The Principal, Agricultural College. (1930.)

207. Marsh, Mr R. W., M.A., Research Station, Long Ashton, Bristol. (1923.)
208. Martyn, Mr E. B., B.A., Department of Agriculture, Georgetown, British Guiana. (1927.)
209. Mason, Mr E. W., M.A., M.Sc., Imperial Bureau of Mycology, 17, Kew Green, Kew, Surrey. (1921.)
210. Mason, Mrs E. W., Suffield House, Paradise Road, Richmond, Surrey. (1922.)
211. Mason, Mr F. A., F.R.M.S., M.S.P.A., 29, Frankland Terrace, Leeds. (1912.)
212. Massey, Mr R. E., F.L.S., Government Botanist, Department of Agriculture, Khartoum North, Sudan. (1929.)
213. Matthews, Professor J. R., M.A., F.L.S., Botanical Department, The University, Reading. (1921.)
214. McDonald, Mr J., B.Sc., Mycologist, Department of Agriculture, Box 323, Nairobi, Kenya Colony, East Africa. (1923.)
215. McFarland, Dr Frank T., Department of Botany, University of Kentucky, Lexington, Ky., U.S.A. (1924.)
216. McLennan, Dr Ethel I., Botanical Department, Melbourne University, Carlton, Victoria, Australia. (1926.)
217. Mehta, Professor K. C., Ph.D., Department of Biology, Agra College, Agra, U.P., India. (1921.)
218. Metcalfe, Mr C. R., B.A., Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey. (1926.)
219. Meulenhoff, Dr J. S., Ruychrocklaan 30, The Hague, Holland. (1921.)
220. Michigan Agricultural College Library, East Lansing, Michigan, U.S.A. (1924.)
221. Millard, Mr W. A., Ph.D., The Agriculture Department, The University, Leeds. (1924.)
222. Missouri, The Botanical Garden, St Louis, Mo., U.S.A. (1902.)
223. Mitra, Mr M., M.Sc., F L.S., Agricultural Research Institute, Pusa, Bihar and Orissa, India. (1928.)
224. Miyabe, Dr Kingo, Professor Emeritus of Botany, Hokkaido Imperial University, Sapporo, Japan. (1919.)
225. Mohendra, Mr K. R., B.Sc. (Agr.), Ph.D., D.I.C., Mycologist to Government, Punjab, Lyallpur, India. (1927.)
226. Montague, Mrs A., Penton, Crediton, N. Devon. (1898.)
227. Montana Experiment Station, Department of Botany and Bacteriology, Bozeman, Montana, U.S.A. (1930.)
228. Moore, Miss E. S., Ph.D., c/o the Secretary, Department of Agriculture, P.O. Box 994, Pretoria, South Africa. (1923.)
229. Moore, Mr W. C., M.A., Ministry of Agriculture, Pathological Laboratory, Milton Road, Harpenden, Herts. (1922.)
230. Morgan, Dr G., Ashley-Hatton, Dyke Road Avenue, Brighton. (1928.)

231. Morris, Mr L. E., Rubber Research Institute, Kuala Lumpur, Federated Malay States. (1924.)
232. Moscow, The Fundamental Bibliothek of the First University of, Mochovaya 9, Moscow, U.S.S.R. (1929.)
233. Moss, Professor C. E., The University, P.O. Box 1176, Johannesburg, South Africa. (1923.)
234. Murphy, Professor P. A., Sc.D., A.R.C.Sc.I., M.R.I.A., Department of Plant Pathology, Albert Agricultural College, Glasnevin, Dublin, N.W. 3. (1924.)
235. Murray, Mr G. H., F.E.S., Director of Agriculture, Rabaul, New Britain, Territory of New Guinea, *via* Australia. (1921.)
236. Murrell, Major Percy J., O.B.E., F.R.M.S., "Littlecroft," Orpington, Kent. (1923.)
237. Muskett, Mr A. E., M.Sc., A.R.C.S., Queen's University, Belfast, North Ireland. (1923.)
238. National Collection of Type Cultures, Curator, Lister Institute, Chelsea Gardens, London, S.W. 7. (1921.)
239. National Museum of Wales, Cardiff. (1924.)
240. Nattrass, Mr R. M., B.Sc. (Agric.), Ph.D., Department of Agriculture, Nicosia, Cyprus. (1925.)
241. Nebraska, The Library, University of, Lincoln, Nebr., U.S.A. (1924.)
242. Nederlandsche Mycologische Vereeniging, c/o Mr A. C. S. Schweers, Nassaulaan 17, Alkmaar, Holland. (1920.)
243. New York Botanical Garden, Bronx Park, New York, U.S.A. (1904.)
244. Nicholson, Mr W. E., F.L.S., 50, St Anne's Crescent, Lewes. (1913.)
245. Nitimargi, Mr N. M., M.Ag. (Bombay), Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1930.)
246. Noel, Miss E. F., F.L.S., 37, Moscow Court, Queen's Road, London, W. 2. (1913.)
247. Norman, Mr L. Stafford, Konjeni Estate, Luchenza P.O., Nyasaland. (1927.)
248. North Carolina, Library, University of, Chapel Hill, North Carolina, U.S.A. (1920.)
249. Nursery and Market Garden Industries' Development Society, Ltd., Experimental and Research Station, Cheshunt, Herts. (1922.)
250. O'Connor, Mr P., B.Sc., A.R.C.Sc.I., College of Science, Upper Merrion Street, Dublin. (1925.)
251. Ogilvie, Mr L., M.A., M.Sc., Research Station, Long Ashton, Nr Bristol. (1922.)
252. Oke, Mr Alfred William, B.A., F.G.S., F.L.S., 32, Denmark Road, Hove, Sussex. (1908.)

253. Ontario Agricultural College, Library, Guelph, Ontario, Canada. (1920.)
254. Osborn, Professor T. G. B., M.Sc., Botanical Department, The University, Sydney, N.S.W., Australia. (1910.)
255. Ottawa, Ontario, Canada, The Library, Geological Survey. (1926.)
256. Overholts, Dr L. O., Botany Department, Pennsylvania State College, State College, Pa., U.S.A. (1929.)
257. Page, Miss W. M., B.Sc., 19, Ledam Buildings, Bourne Estate, Holborn, London, E.C. 1. (1921.)
258. Park, Mr M., Department of Agriculture, Peradeniya, Ceylon. (1929.)
259. Parke Davis & Co., Librarian, Research Department, Detroit, Michigan, U.S.A. (1920.)
260. Paul, Mr W. R. C., M.Sc., D.I.C., F.L.S., Department of Agriculture, Peradeniya, Ceylon. (1928.)
261. Paulson, Mr Robert, F.L.S., F.R.M.S., Glenroy, Cecil Park, Pinner, Middlesex. (1918.)
262. Peacock, Dr H. G., The Lawn, Torquay. (1896.)
263. Pearson, Mr Arthur A., F.L.S., 59, Southwark Street, London, S.E. 1. (1911.)
264. Peklo, Dr Jaroslav, Professor of Applied Botany, Bohemian Technical University, Charles Square, Prague II, Czechoslovakia. (1924.)
265. Perthshire Society of Natural Science, c/o Mr James Winter (Hon. Treasurer), 35, George Street, Perth. (1919.)
266. Petch, Mr T., B.A., B.Sc., Stoney Cross, The Chase, King's Lynn, Norfolk. (1911.)
267. Pethybridge, Mr G. H., Ph.D., B.Sc., Ministry of Agriculture, Pathological Laboratory, Milton Road, Harpenden, Herts. (1919.)
268. Philadelphia, The Academy of Natural Sciences of Philadelphia, Logan Square, Phil., U.S.A. (1925.)
269. Phillips, Dr H. H., 6, St John's Road, Penge, London, S.E. 10. (1923.)
270. Phillips, Mr J. F. V., B.Sc. (For.), D.Sc. (Edin.), Botanist (Tsetse Research), Game Preservation Department, Kondoa-Irangi Tanganyika Territory, East Africa. (1921.)
271. Ping, Mr A. Wentworth, M.A., "St Olave's," Clifton, York. (1926.)
272. Plowright, Mr C. T. M., B.A., M.B., King Street, King's Lynn. (1901.)
273. Potter, Rev. M. C., Sc.D., M.A., F.L.S., Corley Croft, New Milton, Hants. (1896.)
274. Povah, Professor A. H., Farlow Herbarium, 20, Divinity Avenue, Cambridge 38, Mass., U.S.A. (1924.)

275. Preston, Mr N. C., B.Sc., Harper Adams Agricultural College, Newport, Salop. (1920.)
276. Pretoria, South Africa, The Chief, Division of Botany (91403), Department of Agriculture. (1922.)
277. Priestley, Professor J. H., D.S.O., B.Sc., F.L.S., Botanical Department, The University, Leeds. (1912.)
278. Proefstation voor Thee, Departement van Landbouw, Buitenzorg, Java. (1926.)
279. Pusa, Imperial Mycologist, Imperial Agricultural Research Institute, Pusa, Bihar, India. (1921.)
280. Ramsbottom, Mr J., O.B.E., M.A., F.L.S., British Museum, Cromwell Road, South Kensington, London, S.W. 7. (1910.)
281. Ray, Miss Anne, Penarwyn, Gorran Haven, Gorran, Cornwall. (1929.)
282. Rayner, Mr J. F., Swaythling, Southampton. (1902.)
283. Rayner, Dr M. Cheveley (Mrs Neilson Jones), Bedford College for Women, Regent's Park, London, N.W. 1. (1921.)
284. Rea, Miss M. W., M.Sc., Salem House, Sydenham, Belfast, Ireland. (1920.)
285. Rees, Mr John, M.Sc., Adviser in Agricultural Botany, University College, Cardiff. (1929.)
286. Reichert, Dr Israel, Plant Pathologist, Palestine Zionist Executive Agricultural Experiment Station, Tel-Aviv, Palestine. (1924.)
287. Rhind, Mr Donald, B.Sc., Economic Botanist, Department of Agriculture, Agricultural College, Mandalay, Burma. (1922.)
288. Rhodes, Miss Mabel, Lister Institute, Chelsea Gardens, London, S.W. 1. (1921.)
289. Rhodes, Rev. P. G. M., St Mary's, Evesham, Worcestershire. (1929.)
290. Richards, Mr R M., M.B.E., A.R.C.S., F.L.S., The Laboratory, Caledonia Estate, Province Wellesley, Straits Settlements. (1915.)
291. Robson, Mr R., M.Sc., F.Z.S., East Hammingfield, Chelmsford, Essex. (1914.)
292. Roper, Miss Ida M., F.L.S., 4, Woodfield Road, Redland, Bristol. (1921.)
293. Rothamsted Experimental Station, Department of Mycology, Harpenden, Herts. (1923.)
294. Rutgers College and State University of New Jersey, Library, New Brunswick, New Jersey, U.S.A. (1922.)
295. Ryan, Mr G. M., F.L.S., 35, Ladbroke Gardens, London, W. 11. (1923.)
296. St Paul, Minnesota, U.S.A., The Library, Department of Agriculture, University Farm. (1920.)

297. Salisbury, Professor E. J., D.Sc., F.L.S., Botanical Department, University College, Gower Street, London, W.C. 1. (1921.)
298. Salmon, Professor E. S., F.L.S., South-Eastern Agricultural College, Wye, Kent. (1922.)
299. Sampson, Miss K., B.Sc., University College, Aberystwyth, North Wales. (1920.)
300. Samuel, Mr Geoffrey, The University of Adelaide, South Australia. (1923.)
301. Sanderson, Mr A. R., F.L.S., 163, Ampang Road, Kuala Lumpur, Federated Malay States. (1921.)
302. Sawhney, Mr A., M.Sc., Panjab University, Lahore, India. (1927.)
303. Science Library, South Kensington, London, S.W. 7. (1924.)
304. Scott, Mr W. W., Highwood, Speen, Princes Risborough, Bucks. (1922.)
305. Searle, Mr G. Odell, B.Sc. (Agric.), Research Botanist, Linen Industry Research Association, Glenmore House, Lambeg, Lisburn, Ireland. (1920.)
306. Seth, Mr N. L., B.Sc. (Punjab), Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1930.)
307. Sharpe, Mr C. J., Brambleside, Manor Road, Sidcup. (1905.)
308. Sharples, Mr A., A.R.C.S., D.I.C., Mycologist, Department of Agriculture, Kuala Lumpur, Federated Malay States. (1924.)
309. Shaw, Mr F. J. F., D.Sc., A.R.C.S., F.L.S., Imperial Agricultural Research Institute, Pusa, Bihar, India. (1920.)
310. Small, Mr W., M.B.E., M.A., Ph.D., B.Sc., Director, Department of Agriculture, Zomba, Nyasaland. (1915.)
311. Smart, Miss V., High Street, Littlehampton, Sussex. (1929.)
312. Smith, Mr Alexander, M.A., Ph.D., Ministry of Agriculture, Pathological Laboratory, Milton Road, Harpenden, Herts. (1924.)
313. Smith, Mr F. E. V., B.Sc., Microbiologist, Department of Agriculture, Jamaica, B.W.I. (1922.)
314. Smith, Miss K. E., 64, Coton Road, Nuneaton. (1913.)
315. Smith, Professor Noel J. G., Ph.D., B.Sc., Botany Department, Rhodes University College, Grahamstown, S. Africa. (1924.)
316. Smith, Mr Rupert, 38, Greenhill Gardens, Edinburgh. (1927.)
317. Smith, Miss S. Somerford, Albemarle Court Hotel, Leinster Gardens, Lancaster Gate, London, W. 2. (1923.)
318. Solberg, Miss Louise, Universitetets Botaniska Laboratorium, Kristian IV's gate 1, Oslo, Norway. (1923.)
319. South London Botanical Institute, 323, Norwood Road, Tulse Hill, London, S.E. 24. (1921.)

320. Stakman, Professor E. C., University of Minnesota, Minneapolis, Minn., U.S.A. (1922.)
321. Statham, Miss E. M., 262, Burrage Road, Woolwich, London, S.E. 18. (1926.)
322. Stationery Office, H.M., Superintendent of Publications, Book Dept., Westminster, S.W. 1. (3 subscriptions.) (1920.)
323. Stephens, Miss E. L., B.A., Department of Botany, University of Cape Town, Cape Town, South Africa. (1928.)
324. Stephens, Miss F. L., M.Sc., Department of Botany, British Museum (Natural History), Cromwell Road, South Kensington, London, S.W. 7. (1930.)
325. Stirrup, Mr H. H., M.Sc., Midland Agricultural College, Sutton Bonington, Loughborough. (1922.)
326. Storey, Mr H. H., M.A., Ph.D., East African Agricultural Research Institute, Amani, Tanganyika Territory, East Africa. (1922.)
327. Sutherland, Mr G. K., M.A., D.Sc., F.L.S., "Bremhill," 21, Combe Park, Bath, Somerset. (1914.)
328. Swansea Field Naturalists' Society, c/o Mr Alan Stuart, M.Sc., University College, Singleton, Swansea, South Wales. (1924.)
329. Swanton, Mr E. W., A.L.S., Educational Museum, Haslemere, Surrey. (1899.)
330. Swedish Academy of Sciences, Royal, Stockholm, Sweden. (1919.)
331. Sydney, Australia, The Librarian, University of. (1922.)
332. Tabor, Mr R. J., B.Sc., F.L.S., Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1914.)
333. Tagg, Mr H. F., F.L.S., Royal Botanic Garden, Edinburgh. (1921.)
334. Tandy, Mr Geoffrey, B.A., F.L.S., Department of Botany, British Museum, Cromwell Road, South Kensington, London, S.W. 7. (1925.)
335. Taylor, Miss B. K., 98, Cheyne Walk, Chelsea, London, S.W. 3. (1910.)
336. Tennessee, University of, Agricultural Experiment Station, Library, Knoxville, Tennessee, U.S.A. (1926.)
337. Tetley, Miss U., Leyfield, Kirkby Lonsdale, Westmorland. (1929.)
338. Thompson, Miss N. L., B.Sc., 27, Rusholme Road, Putney Hill, London, S.W. 15. (1926.)
339. Tomkins, Mr R. G., B.A., Trinity College, Cambridge. (1925.)
340. United States Department of Agriculture, c/o Wheldon and Wesley, 2–4 Arthur Street, New Oxford Street, London, W.C. 2. (1907.)

341. Vanterpool, Mr T. C., M.Sc., Botanical Department, University of Saskatchewan, Saskatoon, Canada. (1929.)
342. Vasudeva, Mr R. S., Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1929.)
343. Vines, Professor S. H., M.A., D.Sc., F.R.S., F.L.S., Langstone, Exmouth, Devon. (1915.)
344. Wadham, Professor S. M., M.A., Department of Agriculture, The University, Melbourne, Victoria, Australia. (1922.)
345. Wakefield, Miss E. M., M.A., F.L.S., Herbarium, Royal Botanic Gardens, Kew. (1911.)
346. Waldie, Mr J. S. L., B.Sc., C.D.A., Department of Agricultural Botany, The University, Reading. (1925.)
347. Wales, University College of, Librarian, Botanical Department, Aberystwyth, North Wales. (1927.)
348. Wallace, Mr G. B., B.Sc. (Agric.), Ph.D., Department of Agriculture, Morogoro, Tanganyika Territory, East Africa. (1928.)
349. Wallace, Mrs G. B., B.Sc., Morogoro, Tanganyika Territory, East Africa. (1924.)
350. Wallis, Mr A., Westacre, Station Road, Kettering. (1921.)
351. Ware, Mr W. M., M.Sc., South-Eastern Agricultural College, Wye, Kent. (1924.)
352. Washington, Library, State College of Washington, Pullman, Wash., U.S.A. (1924.)
353. Waterhouse, Miss G. M., B.Sc., 35, Southdean Gardens, London, S.W. 19. (1927.)
354. Watson, Mr W., D.Sc., A.L.S., Taunton School, Taunton. (1923.)
355. Welsford, Miss E. J., The Laboratory, Dell Park, Englefield Green, Surrey. (1924.)
356. Westerdijk, Professor Johanna, Javalaan 4, Baarn, Holland. (1923.)
357. Weston, Mr W. A. R. Dillon, M.A., School of Agriculture, Cambridge. (1923.)
358. Whetzel, Professor H. H., M.A., New York State College of Agriculture, Cornell University, Ithaca, N.Y., U.S.A. (1914.)
359. Whitaker, Mr F. Owen, 45, Elmdene Road, Plumstead, London, S.E. 18. (1921.)
360. Whitehead, Mr T., D.Sc., A.R.C.S., University College of North Wales, Bangor. (1920.)
361. Wilkins, Mr W. H., M.A., Department of Botany, The University, Oxford. (1928.)
362. Williams, Mr P. H., 4, Belmont Villas, Windmill Lane, Cheshunt, Herts. (1930.)
363. Williamson, Mrs H. S., B.Sc., 3, Verulam Buildings, Gray's Inn, London, W.C. 1. (1921.)

364. Wilson, Miss A. P., M.B.E., A.R.C.S., 116 Fellows Road, N.W. (1929.)
365. Wilson, Mr Malcolm, D.Sc., A.R.C.S., F.L.S., Royal Botanic Garden, Edinburgh. (1921.)
366. Wiltshire, Mr S. P., M.A., Imperial Bureau of Mycology, 17, Kew Green, Kew, Surrey. (1920.)
367. Wiltshire, Mrs S. P., 24, Lawn Crescent, Kew Gardens, Surrey. (1925.)
368. Wisconsin, The Library, University of, Madison, Wis., U.S.A. (1923.)
369. Wolf, Mr B. L., N.D.A., Cornwall Buildings, 45, Newhall Street, Birmingham. (1923.)
370. Woodcock, Mr A. J. A., M.Sc., F.E.S., Clifton Manor, York. (1926.)
371. Woodward, Mr R. C., Ph.D., School of Rural Economy, Oxford. (1924.)
372. Woolhope, The Naturalists' Field Club, Hereford, c/o Col. M. J. G. Scobie, 2, Offa Street, Hereford. (1896.)
373. Worcestershire Naturalists' Field Club, c/o Mr W. J. Else, Victoria Institute, Worcester. (1921.)
374. Wormald, Mr H., D.Sc., A.R.C.S., Research Station, East Malling, Kent. (1921.)
375. Wright, Mr E. Barton, B.Sc., Botanical Department, King's College, Strand, London, W.C. 2. (1926.)
376. Yale University, Library, New Haven, Connecticut, U.S.A. (1930.)
377. Young, Miss Elaine M., University of the Witwatersrand, Johannesburg, South Africa. (1927.)
378. Zundel, Dr G. L. I., Botany Building, Pennsylvania State College, State College, Pa., U.S.A. (1929.)
379. Zürich, Switzerland, Botanical Garden and Museum, c/o Dr A. U. Däniker. (1921.)

RULES.

Society's name and objects.

1. The Society shall be called "The British Mycological Society," and its object shall be the study of Mycology in all its branches.

Members of Society.

2. The Society shall consist of Honorary Members, Foundation Members and Ordinary Members; the number of Honorary Members shall be limited to 20, and that of Foundation Members to 100, but the number of Ordinary Members shall be unlimited.

Honorary Members.

3. Honorary Members shall be persons of pre-eminence in Mycology, or who have rendered special service to the Society.

Foundation Members.

4. Foundation Members shall be those Members or Societies who joined the Society previous to the limit of 100 Members having been attained*.

Officers.

5. The Officers of the Society shall consist of a President, one or more Vice-Presidents, Treasurer, Secretaries, and Editor or Editors. They shall be elected annually, at the Annual General Meeting of the Society.

Government of Society.

6. The government of the Society shall be vested in a Council, which shall consist of the President and other Officers for the time being, together with two or more other Members who shall be elected annually at the General Meeting, and one-half of whom shall retire each year and not be eligible for immediate re-election. The Members to retire shall be those who have been longest in office or, in case of equality, shall be determined by ballot. Ex-Presidents are *ex-officio* Members of the Council.

Every Meeting of the Council shall be duly summoned by the Hon. Secretary by at least seven days' notice in writing to each Member of the Council.

* The limit of 100 Foundation Members was reached 22nd Oct., 1903.

Period of Office.

7. The Officers and Council shall hold office as from the 1st of January following their election.

Election of Members.

8. Honorary Members shall only be elected at a Meeting of the Society by a majority of the Members then present.

All Ordinary Members shall be proposed and seconded respectively by existing Members, who shall sign a certificate (see Appendix) of recommendation, one at least of the proposers so certifying from personal knowledge. Every candidate for election shall sign an undertaking to abide by the Rules if elected (see Appendix). They shall be elected by a majority of the Members present at any meeting of the Society or by the President and Officers of the Society.

Subscription.

9. All Ordinary Members and Societies shall pay an annual subscription of one pound, and Foundation Members five shillings, due on the 1st of January in each year. Honorary Members shall be exempt from any annual subscription.

Any Member wishing to retire from the Society shall give notice to the Hon. Secretary or Treasurer in writing before the 1st of December of the previous year.

Meetings.

10. The Society shall hold one or more meetings annually, at a place and time determined by the Members at the preceeding Annual General Meeting, or by the Council. The Annual General Meeting for the election of officers and the transaction of other business shall coincide with the Autumn Foray.

Accounts.

11. At the Annual General Meeting of the Society in each year the Hon. Treasurer shall present duly audited accounts.

Alteration of Rules.

12. The Rules shall not be altered except by a two-thirds majority of the Members present at an Annual General Meeting. A printed copy shall be sent to every Member of the Society on election, and in the event of alterations to all Members.

APPENDIX.

Form of proposal for Ordinary Membership of the British Mycological Society.

.....

of.....

.....

being desirous of becoming an Ordinary Member of the British Mycological Society, we, the undersigned Members of the Society, certify that we consider h to be a desirable Member of the Society, and beg to recommend h for election.

Dated this day of 19

.....(From personal knowledge).

Certificate to be signed by the Candidate.

I hereby certify that I desire to become an Ordinary Member of the British Mycological Society and that I will abide by the Rules if elected.

.....

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